Short communication

Effects of the introduced parasite *Philornis downsi* on nestling growth and mortality in the medium ground finch (*Geospiza fortis*)

Sarah K. Huber*

Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, 319 Morrill Science Center, Amherst, MA 01003, USA

**ABSTRACT**

Invasive species have the potential to detrimentally affect native ecosystems by out competing or directly preying upon native organisms, and have been implicated in the extinction of endemic populations. One potentially devastating introduced species in the Galápagos Islands is the parasitic fly *Philornis downsi*. As larvae, *P. downsi* parasitize nestling birds and have been associated with high nestling mortality and reduced growth rates. Here I document nestling growth and mortality in a bimodal population of the medium ground finch, *Geospiza fortis*. Observations were conducted over three years, and under variable ecological conditions. Annual parasite prevalence in nests ranged from 64% to 98%, and nestling mortality in nests with parasites ranged from 16% to 37%. Parasite load and parasite load per nestling follow a skewed distribution with many nests having relatively few parasites, and few nests having many. Parasite load, however, was not correlated with onset of breeding, clutch size, the number of nestlings, nestling survival or fledgling success. Parasite load per nestling, on the other hand, was correlated with clutch initiation date and the proportion of nestlings that died in parasitized nests. Neither nestling size nor growth rate differed between parasitized and unparasitized nests. In addition, male and female beak morphology was not correlated with parasite load, breeding variables or nestling survival. Thus, while overall mortality due to parasitism is high, ecological conditions and possible host defenses may potentially counter some of the detrimental affects of *P. downsi* on nestling size and growth. These results taken together suggest that parasitism of *P. downsi* larvae on nestling *G. fortis* has the potential to lead to large population declines.

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biotas are thought to be particularly vulnerable to the negative impacts of invasive species, in part, because island habitats have lower species diversity, with fewer niches exploited by native fauna, and they tend to support small population sizes of endemic organisms (Diamond, 1984; Dobson and McCallum, 1997; Dobson and Foufopoulos, 2001; Altizer et al., 2001; Vitousek, 2002).

The Galápagos Islands of Ecuador have served as an excellent model system for the study of ecology and evolution (Grant, 1999; Wikelski, 2005; Arbogast et al., 2006). However, an increasing number of invasive species are threatening native biotas (Wikelski et al., 2004; Causton et al., 2006; Parker et al., 2006), with a recent count estimating the number of exotic species to be over 800 (Bensted-Smith et al., 2000). One potentially devastating invasive species is the fly Philornis downsi, which in the larval stage is a hematophagous parasite of nestling birds. In 1964 several specimens of P. downsi were collected in the Galápagos Islands (Causton et al., 2006). Additional collections were made in 1981; however, the presence of P. downsi went relatively unnoticed until 1997, when larvae were discovered in the nests of land birds (Fessl et al., 2001).

To date, P. downsi has been found to parasitize at least 12 bird species in the Galápagos Islands (Fessl and Tebbich, 2002), and has been recorded from 13 to 15 major islands (Wiedenfeld et al., 2007). Philornis downsi has been implicated in the decline of populations of the mangrove finch, Cactospiza pallida, and the warbler finch, Certhidea olivacea (Dvorak et al., 2004; Grant et al., 2005).

Flies of the genus Philornis are common throughout the Neotropics (Dodge, 1955, 1963, 1968; Dodge and Aitkin, 1968; Couri, 1984, 1986). Females presumably lay their eggs directly on nestlings (Meinert, 1890; Dodge, 1971; Arendt, 1985), and larvae feed on the blood and fluid of nestlings. The early instars will often burrow in the nostrils of nestlings, causing long term morphological damage (Fessl et al., 2006a). Later instars live in the nesting material and surface at night to feed on nestlings. Philornis downsi parasitism has been correlated with a reduction in nestling survival in several species of Darwin’s finches, including the woodpecker finch (Cactospiza pallida), small tree finch (Camarhynchus parvulus), warbler finch (C. olivacea), small ground finch (Geospiza fuliginosa), and medium ground finch (Geospiza fortis) (Fessl and Tebbich, 2002; Fessl et al., 2006b). Parasitism by P. downsi also has been found to impact negatively nestling growth rates in a combined analysis of small ground finches and medium ground finches (Fessl et al., 2006b), and result in reduced hemoglobin and immature red blood cell counts in the small ground finch (Dudaniec et al., 2006).

This study documents the impacts of P. downsi parasitism on nestling survival and growth in the medium ground finch, G. fortis, at El Garrapatero, Santa Cruz Island, Galápagos (Fig. 1). Interestingly, the population of G. fortis at El Garrapatero is bimodal with respect to beak morphology, with birds falling mainly into large and small beak size classes with relatively few intermediates (Hendry et al., 2006; Huber and Podos, 2006). As in other populations of G. fortis (Grant and Grant, 2006; Grant, 1999; Price, 1987; Keller et al., 2001), beak size variation likely has a strong additive genetic basis and reflects selection imposed by variation in the size and hardness of seeds. The bimodality is likely due to specialization by the two morphs on different food types, perhaps coupled with intra- or inter-specific competition. Indeed, intermediate birds survive at lower rates between years in comparison to large and small morphs (A.P. Hendry et al., unpublished data). In addition to determining the effects of P. downsi parasitism on nestling growth and mortality, I will test whether beak size confers a selective advantage with respect to parasitism.

2. Materials and methods

2.1. Parasite prevalence and nestling mortality

Research was conducted at El Garrapatero, Isla Santa Cruz, Galápagos, Ecuador (Fig. 1, GPS coordinates S 00°40’20”–41’20”; W 90°13’10”–14’40”). Nests of G. fortis were observed from January to April 2004, January to May 2005, and January to March 2006. The average monthly rainfall during these periods was collected by weather stations at the Charles Darwin Research Station in Academy Bay (Fig. 1).

In 2004, the fate of each nest was recorded as “successful” (nestlings fledged) or “failed” (nestlings were predated or found dead in the nest). No data was collected on rates of predation or parasitism; however, dead nestlings were examined for P. downsi larvae and the presence of lesions associated with larval feeding.

In 2005, nests were located, and checked every 3–4 days during the breeding season. During each nest check the
number of eggs or nestlings was recorded, and nestlings were inspected for external signs of parasites (e.g., lesions on the body). A decrease in the number of eggs or nestlings from one visit to the next was presumed to be the result of predation. Predators of Darwin’s finches include mockingbirds, owls, and in some cases rats (Grant, 1999). There is no evidence to suggest that eggs are ejected by Darwin’s finch adults or nestlings, and visual inspection of the ground under predated nests in this study failed to recover any eggs. When nests were no longer active (e.g., due to predation, the death of nestlings, or fledging), nests were collected and the number of P. downsi larvae and pupae per nest were recorded. Because larvae feed at night, it was not possible to determine the number of parasites infecting a given nestling within a nest. Therefore, to determine parasite load per nestling, I divided the total number of parasites by the number of nestlings in the nest. In summary, I recorded for each nest: clutch initiation date, clutch size, the number of eggs predicted, the number of nestlings predated, the number of nestlings fledged, the parasite load, and the parasite load per nestling.

In 2006, nests were checked every other day and the number of eggs and nestlings recorded. Birds were again examined for the presence of lesions associated with P. downsi larval feeding. I recorded for each nest: clutch initiation date, clutch size, the number of eggs predated, the number of nestlings predated, the number of nestlings dead in the nest, the number of nestlings fledged, the parasite load, and whether parasites were present or absent. The number of nests with P. downsi larvae was recorded, but the number of larvae per nest (parasite load) was not determined.

Observations of nesting survival were terminated prior to the end of the breeding season in 2005 and 2006. At the end of the observation period in 2005, the fate of 12 nestlings from four nests was unknown. At the end of the observation period in 2006, the fate of 10 nestlings from five nests was unknown. These 22 nestlings were removed from further analyses.

2.2. Nestling size and growth rate

Data on nestling size and growth rate was collected in 2006 only. Individual nestlings within a nest were marked with a unique colored plastic leg band, or by coloring a toenail with non-toxic paint. Nestlings were measured every other day, and measurements included: mass, tarsus, gape, beak length, beak width, and beak depth.

For measures of both size and growth rate the mean value of nestlings within a nest was used for statistical analysis. This is because siblings are genetically similar, and thus statistically non-independent. The mean size of nestlings within a nest was determined for each day post hatching (1 day old, 2 days old, etc.). Nestlings hatch asynchronously, and so measurements were collected at days one, three, five, etc., for some nestlings within a nest, and days two, four, six, etc., for other nestlings within the same nest. Because nesting mortality was high, in some nests only a single nestling was measured at given age.

The size of parasitized nestlings at each age was then plotted against the size of unparasitized nestlings of the same age for all morphological variables. To determine the size and growth trajectories of nestlings from parasitized to unparasitized nests, I used reduced major axis regression (RMA). A RMA that results in a regression line with a slope of one would indicate that size at a given age is not statistically different between parasitized and unparasitized nestlings.

Growth rates were determined for individual nestlings by calculating the average change in a variable per day. Growth rates were then averaged across all nestlings in a nest. Due to high nestling mortality, growth rates could be calculated for two unparasitized nests and seven parasitized nests. A Kruskal–Wallis test was used to compare median growth rates between parasitized and unparasitized nests for each variable.

2.3. Adult beak morphology

Adult birds were captured in mist nets and banded with unique combinations of one metal and three color bands. The following measurements were taken from each bird, as in Grant et al. (1985): beak length, beak depth, and beak width. The first axis of a principle component analysis (PC1) that included beak length, beak depth, and beak width was used in future analyses of adult beak morphology. Birds were classified into three beak sizes classes (small, intermediate, and large) based on an hierarchical cluster analysis of PC1 (for methods see Huber et al. (2007)). A χ-square test was used to determine if the beak size of breeding birds was representative of the population as a whole.

To test for the influence of parental beak morphology on nestling mortality and parasite loads I correlated male and female beak PC1 scores from 2005 with clutch initiation date, clutch size, number of nestlings, number of dead nestlings in nests with parasites, proportion of dead nestlings in nests with parasites, number of nestlings fledged, proportion of nestlings fledged, parasite load, and parasite load per nestling. Male and female beak PC1 scores from 2006 were correlated with clutch initiation date, clutch size, and number of nestlings. Sample sizes were too low in 2006 to correlate beak morphology with the number of dead nestlings in nests with parasites (n = 3 nests), the proportion of dead nestlings in nests with parasites (n = 3 nests), the number of nestlings fledged (n = 1 nest), or the proportion of nestlings fledged (n = 1 nest). In 2006, parasite load was not determined. Rather, the presence or absence of parasites was assessed. A logistic regression was used to determine if beak morphology was a predictor of parasite presence or absence.

The collection of data in this study was done in concordance with animal use protocols approved by the University of Massachusetts Amherst.

3. Results

3.1. Parasitism and nestling mortality

High nestling mortality occurred in all three years of this study. In 2004, 100% of nests failed: all nestlings were predated or were found dead in the nest. Dead nestlings had lesions indicative of larval feeding by P. downsi, and larvae or pupae were found in the nestling material of all nests with dead nestlings. In 2005, nestling mortality associated with
parasitism was high, though not as high as predation rates, and larvae and pupae of P. downsi were found in all nests that contained dead nestlings (Table 1). Larvae were frequently found feeding inside the head and body cavity of dead nestlings. In 2006, fewer nestlings died in nests with parasites (Table 1). However, many nestlings that were ultimately predated also showed signs of P. downsi parasitism (e.g., lesions on body and/or larvae and pupae in empty nest).

Parasite load per nest follows a skewed distribution, common in many parasite systems (Fig. 2a), even when standardized for the number of nestlings per nest (Fig. 2b). However, parasite load was not a significant predictor of any breeding variables, nestling mortality, or fledging (Table 2). Parasite load per nestling was significantly correlated with clutch initiation date (Table 2). Nests earlier in the breeding season had significantly more parasites per nestling than did nests later in the breeding season. This is likely because clutch initiation date has a significant, positive relationship with clutch size ($F = 39.66$, $R = 0.76$, $p < 0.001$); clutch sizes were higher later in the breeding season. Parasite load per nestling also was significantly correlated with the proportion of nestlings in a nest that died; nests with a higher number of parasites per nestling had a larger proportion of nestlings die (Table 2).

<table>
<thead>
<tr>
<th>Table 1 – Summary of parasite prevalence and nestling mortality in G. fortis</th>
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<td></td>
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<tr>
<td>2005</td>
</tr>
<tr>
<td>Number of nests with nestlings</td>
</tr>
<tr>
<td>Number of nests with parasites</td>
</tr>
<tr>
<td>Number of nests</td>
</tr>
<tr>
<td>Number of nestlings</td>
</tr>
<tr>
<td>Number of nestlings predated</td>
</tr>
<tr>
<td>Number of nestlings in nests with parasites</td>
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<tr>
<td>Number of dead nestlings in nests with parasites</td>
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<td>Number dead nestlings</td>
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<tr>
<td>Number of nestlings predated</td>
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<tr>
<td>Number dead nestlings in nests with parasites</td>
</tr>
<tr>
<td>Number fledged</td>
</tr>
<tr>
<td>Number of nests with nestlings</td>
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<td>Number of nests with parasites</td>
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<td>Number of nests</td>
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<td>Number of nestlings predated</td>
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<tr>
<td>Number of nestlings in nests with parasites</td>
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<tr>
<td>Number of dead nestlings in nests with parasites</td>
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<tr>
<td>Number of dead nestlings</td>
</tr>
<tr>
<td>Number of nestlings predated</td>
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<tr>
<td>Number of nestlings</td>
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<tr>
<td>Number of nestlings</td>
</tr>
</tbody>
</table>

3.2. Nestling size and growth rate

Nestlings from parasitized and unparasitized nests were similar in size throughout the nestling period (Fig. 3). The results of a reduced major axis regression reveal no difference in size between parasitized and unparasitized nestlings in mass, tarsus, beak gape, beak length, or beak width (Table 3). In all cases, except beak depth, the 95% confidence intervals of the slopes include one. Beak depth is the only variable for which the 95% confidence intervals do not encompass a slope of one. Young birds have similar beak depths; however, as nestlings get older the beak depth of unparasitized birds tends to be larger than that of unparasitized birds (Fig. 3).

Mean growth rates of nestlings in parasitized and unparasitized nests were not significantly different for any of the six variables measured (Fig. 4; mass: $\chi^2 = 0.86$, $P = 0.77$; tarsus: $\chi^2 = 0.54$, $P = 0.46$; gape: $\chi^2 = 0.78$, $P = 0.38$; beak length: $\chi^2 = 0.09$, $P = 0.77$; beak depth: $\chi^2 = 0.78$, $P = 0.38$; and beak width: $\chi^2 = 0.10$, $P = 0.38$).

3.3. Ecological conditions and nestling mortality

In 2004, 100% of observed nestlings died, and this was one of the driest breeding seasons on record (total rain January–May = 51.1 mm). The early part of the breeding season in 2005 was also extremely dry. In February 0.2 mm of rain fell, and only six pairs bred. Of those, four out of six nests produced nestlings. Heavy rains fell from March 9 to 15 (109.2 mm), with little to no rain falling after March 15. Very little rain fell in April (0.8 mm). After the rains, breeding was synchronous with two periods in which nestlings were present in nests: March 27–April 16 and April 28–May 10.

In 2005, mortality in nests with parasites was highest in February (86%: six out of seven nestlings), followed by the second cohort after the rain, April 28–May 10 (46%: 19 out of 41 nestlings). The first cohort of nestlings to hatch after the rain,
Table 2 – Results of a Pearson correlation of parasite load and parasite load per nestling with breeding variables, nestling mortality, and fledging success (N = number of nests)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Parasite load</th>
<th>Parasite load per nestling</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>p</td>
</tr>
<tr>
<td>Clutch initiation date</td>
<td>32</td>
<td>-0.28</td>
<td>0.12</td>
</tr>
<tr>
<td>Clutch size</td>
<td>32</td>
<td>-0.11</td>
<td>0.55</td>
</tr>
<tr>
<td>Number of nestlings</td>
<td>32</td>
<td>0.03</td>
<td>0.88</td>
</tr>
<tr>
<td>Number of dead nestlings in nests with parasites</td>
<td>19</td>
<td>0.39</td>
<td>0.10</td>
</tr>
<tr>
<td>Proportion of dead nestlings in nests with parasites</td>
<td>19</td>
<td>0.36</td>
<td>0.13</td>
</tr>
<tr>
<td>Number of nestlings fledged</td>
<td>5</td>
<td>0.31</td>
<td>0.61</td>
</tr>
<tr>
<td>Proportion of nestlings fledged</td>
<td>5</td>
<td>0.31</td>
<td>0.61</td>
</tr>
</tbody>
</table>

Values in bold are statistically significant.

Fig. 3 – Size of parasitized and unparasitized nestlings at days 1–8 and day 11. The dashed line has an intercept through the origin and a slope of one. Points falling on this line indicate that the size of parasitized and unparasitized nestlings is equal.

from March 27 to April 16, had the lowest nestling mortality (29%: 23 out of 81 nestlings). Fledglings were recorded only from this cohort (12%: 10 out of 81 nestlings fledged). However, when observations came to an end in May, 12 nestlings were still alive. The fate of these nestling is unknown, although all had visual signs of parasites.
Parasite load was variable across nests with many nests having relatively few parasites and a few nests having many parasites (Fig. 2). This distribution is a common feature of many host-parasite systems (Anderson and Gordon, 1982). Parasite load was not correlated with any aspects of host breeding behavior or nestling mortality in this system (Table 2). However, when parasite load was calculated as a function of the number of nestlings in the nest, it was correlated with clutch initiation date (Table 2). This result suggests that birds which breed first might be more vulnerable to parasitism than later nesting birds, and stands in contrast to previous studies of hematothaphagic parasites in other species of birds which found no relationship between parasite load and date of clutch initiation (Hurtrez-Bousses et al., 1999). Parasite load per nestling was also correlated with the proportion of nestlings that died in a nest. These results together suggest that selection should favor birds with larger clutch sizes, which would effectively reduce the number of parasites per nestling within the nest.

Nestling size and growth were not found to differ between parasitized and unparasitized nests, a finding that stands in contrast to previous studies of P. downsi parasitism of Darwin’s finches (Fessl et al., 2006b). The failure of this study to detect differences between parasitized and unparasitized nestlings may be due to small samples sizes, as few nests were parasite free. However, variation in ecological conditions might also explain these results. During the Fessl et al. (2006b) study in 2004, very little rain fell, and Santa Cruz experienced one of the most severe droughts in a 40 year period (Grant and Grant, 2006). Starvation and malnourishment potentially contributed to decreased nestling growth rates in parasitized nests. By contrast, late 2005 and 2006 were very wet years, and food resources were abundant. The increased availability and quality of food during these years might have off-set the detrimental effects of parasitism to nestling growth. The 2005 breeding season provides some evidence that rainfall might influence nestling condition. During the wettest part of 2005 (late-March to early-April) nestling mortality due to parasites was the lowest (29%), and this was the only period of time in which nestlings fledged.

The potential evolution of host defenses, such as increased adult provisioning, also may help to explain why growth rates in this study differed from those of Fessl et al. (2006b). Several studies documenting the impacts of hematophagous ectoparasites on nestling growth in other avian-parasite systems have found no difference in size or growth rates between parasitized and unparasitized nestlings (Johnson and Albrecht, 1993; Merino and Potti, 1995; Hurtrez-Bousses et al., 1997; Miller and Fair, 1997). One hypothesis for this result is that adults adjust feeding rates when nestlings are parasitized (Mason, 1944; Johnson and Albrecht, 1993). In

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**Table 3 – Results of a reduced major axis regression of size variables for parasitized and unparasitized nestlings**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Intercept $\pm$ 1 SE</th>
<th>Slope $\pm$ 1 SE</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (g)</td>
<td>$-1.12 \pm 3.45, 1.20$</td>
<td>$1.32 (1.00, 1.64)$</td>
<td>0.93</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>$-0.76 \pm 3.52, 1.99$</td>
<td>$1.12 (0.91, 1.33)$</td>
<td>0.95</td>
</tr>
<tr>
<td>Gape (mm)</td>
<td>$-0.52 \pm 2.98, 1.93$</td>
<td>$1.05 (0.79, 1.31)$</td>
<td>0.92</td>
</tr>
<tr>
<td>Beak length (mm)</td>
<td>$-0.16 \pm 1.05, 0.73$</td>
<td>$1.07 (0.88, 1.27)$</td>
<td>0.96</td>
</tr>
<tr>
<td>Beak depth (mm)</td>
<td>$-0.92 \pm 1.82, 0.01$</td>
<td>$1.26 (1.06, 1.46)$</td>
<td>0.97</td>
</tr>
<tr>
<td>Beak width (mm)</td>
<td>$-0.38 \pm 2.17, 1.41$</td>
<td>$1.12 (0.79, 1.44)$</td>
<td>0.89</td>
</tr>
</tbody>
</table>

The 95% confidence intervals are reported in parentheses.

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**Fig. 4 – Mean nestling growth rate (calculated as the mean change in a variable per day) between parasitized and unparasitized G. fortis nests. Differences are not statistically significant.**

3.4. **Beak morphology and nestling mortality**

Beak morphology was determined for males and females of 38 pairs in 2005 and 15 pairs in 2006. The distribution of beak morphology of breeding adults was representative of the population as a whole (2005: $\chi^2 = 5.08$, p = 0.08; 2006: $\chi^2 = 3.00$, p = 0.22). Beak morphology of males and females was not correlated with any breeding factors in 2005 and 2006 (Table 4), or with nestling mortality and parasite load in 2005 (Table 4). In 2006, only three nests contained dead nestlings, precluding a rigorous statistical test of the relationship between beak morphology and nestling mortality. Parasite prevalence, but not load, was determined for nests in 2006. A logistic regression found that beak morphology was not a significant predictor of parasite prevalence (male beak PC1: N = 13 nests; W = 1.42, p = 0.23 and female beak PC1: N = 13 nests; W = 0.34, p = 0.56).

4. **Discussion**

Nestling mortality in nests with P. downsi larvae was extremely high in G. fortis at El Garrapatero (Table 1). Parasite related mortality, coupled with mortality due to predation, resulted in only 12 fledglings out of 159 nestlings over a three year period. While combined mortality was high in all years, predation of nestlings was much higher in 2006 than in 2005, and nestling mortality in parasitized nests was lower in 2006 than in 2005 (Table 1). However, many of the nestlings that were parasitized were also parasitized by P. downsi. Had predation been lower, many of those nestlings would likely have died due to parasite related causes.

Parasite load was variable across nests with many nests having relatively few parasites and a few nests having many parasites (Fig. 2). This distribution is a common feature of many host-parasite systems (Anderson and Gordon, 1982). Parasite load was not correlated with any aspects of host breeding behavior or nestling mortality in this system (Table 2). However, when parasite load was calculated as a function of the number of nestlings in the nest, it was correlated with clutch initiation date (Table 2). This result suggests that birds which breed first might be more vulnerable to parasitism than later nesting birds, and stands in contrast to previous studies of hematothaphagic parasites in other species of birds which found no relationship between parasite load and date of clutch initiation (Hurtrez-Bousses et al., 1999). Parasite load per nestling was also correlated with the proportion of nestlings that died in a nest. These results together suggest that selection should favor birds with larger clutch sizes, which would effectively reduce the number of parasites per nestling within the nest.

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support of this hypothesis, adult provisioning has been found to increase in nests of blue tits with hematophagous fly larvae (Christie et al., 1996; Triplet and Richner, 1997; Hurtrez-Bous-sès et al., 1998; Banbura et al., 2004). There are currently no data on feeding rates of adult Darwin’s finches with respect to parasite load or ecological conditions.

Previous studies of beak morphology in this population suggest that large and small morphs may have a fitness advantage in comparison to birds with intermediate sized beaks (Hendry et al., 2006; Huber et al., 2007; A.P. Hendry et al., unpublished data). However, beak morphology was unrelated to parasite load. Thus, it appears as though bill morphology does not confer a fitness advantage with respect to parasitism. Interestingly, parasitized nestlings had smaller beak depths than unparasitized nestlings (Table 3, Fig. 3). Selection acts on beak size and shape in response to food availability and inter- and intra-specific competition (Boag and Grant, 1981; Schluter et al., 1985; Grant and Grant, 2006), and beak morphology, in turn, correlates with bite force (Herrel et al., 2005a,b) and acoustic features of songs (Podos, 2001; Huber and Podos, 2006). Thus, parasitized offspring might have reduced fitness after reaching adulthood. In addition, parasitized birds have been found to have deformed beaks as a result of larval feeding in the nasal cavity (Fessl et al., 2006a). These results have interesting implications for how heritability is measured in populations. Heritability estimates are calculated by comparing traits of adults to their offspring. Charmantier et al. (2004) found that nests containing hematophagous fly larvae had decreased heritability estimates of morphological traits in comparison to nests without larvae. Thus, knowledge about parasite prevalence is vital to determining how trait variation is measured across generations in natural populations. The degree to which parasitized nestlings differ from their parents with respect to beak morphology has implications for the stability of the bimodality at El Garrapatero.

In conclusion, the relationship between Darwin’s finches, P. downsi, and finch predators is dynamic. While overall mortality due to parasitism is high, ecological conditions and possible host defenses might have the potential to counter some of the detrimental affects of P. downsi on nestling size and growth. The earliest record of P. downsi on the Galápagos Islands is 1964, and collections made by Peck et al. on Santa Cruz in 1989 contained specimens of P. downsi (Causton et al., 2006). Assuming that P. downsi was present at El Garrapatero during this period, Darwin’s finches may have begun to evolve defenses against parasites in the 40 years ensuing the introduction of P. downsi. Possible host defenses that have not been tested in any population of Darwin’s finches to date include increases in adult provisioning, nestling behavior, and the evolution of a Philornis-specific immune response.

No long term data exist that document interactions between Darwin’s finches and P. downsi in a single population, and in general little is known about the natural history of P. downsi (Dudaniec and Kleindorfer, 2006). Parasitism of P. downsi larvae on nestling G. fortis has the potential to lead to dramatic population declines of Darwin’s finches, not just in this population, but through out the archipelago as a whole (Wiedenfeld et al. 2007; Wikelski et al., 2004). Detailed, long-term research into the dynamics of host-parasite adaptation and coevolution in Darwin’s finches is urgently needed.

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REFERENCES


Table 4 – Pearson correlation coefficients for beak morphology and breeding variables, nestling mortality, and fledging success for 2005 and 2006 (N = number of nests)

<table>
<thead>
<tr>
<th></th>
<th>2005</th>
<th>2006</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male beak PC1</td>
<td>Female beak PC1</td>
</tr>
<tr>
<td>Clutch initiation date</td>
<td>28 0.01 0.06</td>
<td>23 0.18 0.21</td>
</tr>
<tr>
<td>Clutch size</td>
<td>28 −0.15</td>
<td>21 −0.06</td>
</tr>
<tr>
<td>Number of nestlings</td>
<td>26 −0.30</td>
<td>15 0.02</td>
</tr>
<tr>
<td>Number of dead nestlings in nests with parasites</td>
<td>19 −0.29</td>
<td>−0.13</td>
</tr>
<tr>
<td>Number of nestlings fledged</td>
<td>19 −0.36</td>
<td>0.03</td>
</tr>
<tr>
<td>Proportion of nestlings fledged</td>
<td>5 0.68</td>
<td>0.59</td>
</tr>
<tr>
<td>Parasite load</td>
<td>26 −0.002</td>
<td>15 0.15</td>
</tr>
<tr>
<td>Parasite load per nestling</td>
<td>26 0.21</td>
<td>0.34</td>
</tr>
</tbody>
</table>

No correlations were statistically significant (p > 0.05).


Warner, R.E., 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70, 101–120.


