

# Higher body condition with infection by *Haemoproteus* parasites in Bananaquits (*Coereba flaveola*)

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Parasite transmission is a heterogeneous process in host-parasite interactions. This heterogeneity is particularly apparent in vector-borne parasite transmission where the vector adds an additional level of complexity. Haemosporidian parasites, a widespread protist, cause a malaria-like disease in birds globally, but we still have much to learn about the consequences of infection to hosts' health. In the Caribbean, where malarial parasites are endemic, studying host-parasites interactions may give us important insights about energetic trade-offs involved in malarial parasites infections in birds. In this study, we tested the consequences of *Haemoproteus* infection on the Bananaquit, a resident species of Puerto Rico. We also tested for potential sources of individual heterogeneity in the consequences of infection such as host age and sex. To quantify the consequences of infection to hosts' health we compared three complementary body condition indices between infected and uninfected individuals. Our results showed that Bananaquits infected by *Haemoproteus* had higher body condition than uninfected individuals. This result was consistent among the three body condition indices. Still, we found no clear evidence that this effect was mediated by host age or sex. We discuss a set of non-mutually exclusive hypotheses that may explain this pattern including metabolic syndrome, immunological responses leading to host tolerance or resistance to infection, and potential changes in consumption rates. Overall, our results suggest that other mechanisms, may drive the consequences of avian malarial infection.

1 **Higher body condition with infection by *Haemoproteus***  
2 **parasites in Bananaquits (*Coereba flaveola*)**

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10

11 **Abstract**

12 Parasite transmission is a heterogenous process in host-parasite interactions. This  
13 heterogeneity is particularly apparent in vector-borne parasite transmission where the vector adds  
14 an additional level of complexity. Haemosporidian parasites, a widespread protist, cause a  
15 malaria-like disease in birds globally, but we still have much to learn about the consequences of  
16 infection to hosts' health. In the Caribbean, where malarial parasites are endemic, studying host-  
17 parasites interactions may give us important insights about energetic trade-offs involved in  
18 malarial parasites infections in birds. In this study, we tested the consequences of *Haemoproteus*  
19 infection on the Bananaquit, a resident species of Puerto Rico. We also tested for potential  
20 sources of individual heterogeneity in the consequences of infection such as host age and sex. To  
21 quantify the consequences of infection to hosts' health we compared three complementary body  
22 condition indices between infected and uninfected individuals. Our results showed that  
23 Bananaquits infected by *Haemoproteus* had higher body condition than uninfected individuals.  
24 This result was consistent among the three body condition indices. Still, we found no clear

25 evidence that this effect was mediated by host age or sex. We discuss a set of non-mutually  
26 exclusive hypotheses that may explain this pattern including metabolic syndrome,  
27 immunological responses leading to host tolerance or resistance to infection, and potential  
28 changes in consumption rates. Overall, our results suggest that other mechanisms, may drive the  
29 consequences of avian malarial infection.

30 **KEYWORDS:** Birds, Caribbean, heterogeneity, haemosporidian, Puerto Rico, virulence.

## 31 **Introduction**

32 Virulence, or host fitness reduction as a consequence of parasite infection, is often  
33 viewed as an unavoidable cost for parasites that reproduce at the expense of host resources (Bull  
34 1994, Ewald 1994). This traditional understanding of the eco-evolutionary consequences of  
35 parasite infection comes from theoretical models that make simplifying assumptions such as  
36 homogeneous transmission (Anderson and May 1982, Alizon et al. 2009). Still, in nature,  
37 parasite transmission is a heterogeneous process (VanderWaal and Ezenwa 2016). Variability in  
38 parasite transmission strategies, individual traits (i.e., host immunity), and environmental factors  
39 may interact in complex ways resulting in a wide array of consequences to host health (Acevedo  
40 et al. 2019). This is particularly true in vector-borne parasite systems where infected vectors—the  
41 agents of transmission—add a layer of complexity by interacting with the host in heterogeneous  
42 environments (Lachish et al. 2011, Acevedo et al. 2019).

43 Haemosporidian parasites (Order Haemosporida, genera *Plasmodium*, *Haemoproteus*,  
44 and *Leucocytozoon*) are worldwide protists infecting birds of different families, causing a  
45 malaria-like disease (Valkiunas 2014). The impacts of these parasites on birds' host fitness are  
46 generally not well understood with empirical research showing mixed results (e.g., Moller et al.

47 2009, LaPointe et al. 2012, Cornet et al. 2013, Ilgunas et al. 2019, Videval et al. 2020). Malarial  
48 parasites may cause detrimental effects on hosts, such as increasing mortality, and decreasing  
49 overall body condition (e.g., Atkinson et al. 1995). On the other hand, particularly where  
50 haemosporidian parasites are endemic, there might not be any negative reported effects to the  
51 hosts (e.g., Bensch et al. 2007). Multiple mechanisms have been proposed to explain this lack of  
52 negative fitness consequences including immunological strategies such as tolerance and  
53 resistance (Sorci 2013). Within these strategies, strong negative fitness costs are avoided because  
54 the host clears the infection (resistance) or has developed an immune response that allows it to  
55 withstand infection (tolerance).

56 Haemosporidian parasites may have different effects depending on the age and sex of  
57 individuals, such that juveniles tend to develop a more severe infection, and even have higher  
58 mortality compared to adults (Isaksson et al. 2013). For instance, juvenile feral pigeons infected  
59 with *Haemoproteus columbae* are more likely to have increased infection levels and higher  
60 mortality than adults (Sol et al. 2003). The naïve immune system of juveniles can be more  
61 susceptible to infection leading to higher within-host replication rates and higher parasite load  
62 (Padgett and Glasser 2003, Calero-Riestra & Garcia 2016, Hammers et al. 2016). In sex-  
63 dependent studies, infected female Tawny pipits had reduced body condition compared to  
64 infected males (Calero-Riestra & Garcia 2016). This may be related to higher reproductive costs  
65 for females compared to males during the breeding season. Still, the sex-mediated costs of  
66 infection are not necessarily generalizable. A recent meta-analysis showed similar viability to  
67 parasitism among males and females (Hasik and Siepielski 2022).

68 In this study, we assessed the consequences of infection by avian malarial parasites on  
69 host body condition in the most abundant bird species in Puerto Rico and the Caribbean, the

70 Bananaquit (*Coereba flaveola*). Specifically, we asked: (1) do *Haemoproteus*-infected  
71 individuals suffer from reduced body condition when compared to uninfected individuals? and 2)  
72 are related changes in body condition dependent on age or sex? We expected, following  
73 predictions from the classical theory, that infected individuals would have lower body condition  
74 and that this effect would be more pronounced in juveniles and by different by sex. If body  
75 condition decreases with infection, it would provide evidence of negative consequences of  
76 endemic malarial parasites as predicted by the theory (Alizon et al. 2009, Hasik and Siepielski  
77 2022).

## 78 **Materials & Methods**

79 The Caribbean has been proposed as an ideal natural laboratory to study the ecology and  
80 evolution of vector-borne parasite-host interactions (Ricklefs et al. 2016). In the Caribbean,  
81 malarial parasites are endemic, and host species diversity is low, but many species are generalists  
82 occupying a wide variety of habitats (Acevedo and Restrepo 2008). These factors create a unique  
83 set of conditions for host-parasite co-evolution. While multiple studies describe the  
84 biogeographic patterns of malarial parasites of Caribbean bird hosts (e.g., Fallon et al. 2004,  
85 Ricklefs et al. 2016), our understanding of the potential health consequences of malaria infection  
86 to Caribbean bird hosts is limited.

87 We conducted the study from June 2018 to January 2019 in 13 urban forest patches (each  
88 site was visited 1–4 times, Table S1) in the metropolitan area of Puerto Rico, an urbanized area  
89 that comprises 10% of the island (Fig. S1; Table S1) (Martinuzzi et al. 2007). In Puerto Rico,  
90 Bananaquits breed throughout the year with increased reproductive activity between February  
91 and June (Wunderle 1982). We chose Bananaquits (*Coereba flaveola*) as our study species  
92 because it is the most abundant species in urban forests in the Caribbean and previous studies

93 showed that *Plasmodium* and *Haemoproteus* parasites commonly infect this species (Wolff et al.  
94 2018, Antonides et al. 2019). Note that, while we use the basal genus *Haemoproteus* to describe  
95 the parasites in this study, it is likely that these lineages belong to the *Parahaemoproteus*  
96 subgenus (Martinsen et al. 2008). All bird handling procedures were conducted with approval of  
97 the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico  
98 protocol number 3011-02-05-2018, the USGS Federal Bird Banding Permit number 21669, and  
99 the Department of Natural and Environmental Resources of Puerto Rico permit number 2018-IC-  
100 066. All individuals in this study were captured using 2.5m x 6m and 2.5m x 12m mist nets. We  
101 used 4 to 8 mist nets per sampling period. Nets were open by sunrise and closed between 8:30-  
102 10:00 AM depending on sunlight, weather, or presence of raptors. Bananaquits are difficult to  
103 sex and/or age due to their monomorphic plumage. Upon capture, we aged and sexed individuals  
104 using standard procedures such as visual inspection of cloacal protuberance, brood patch, and  
105 skull pneumatization (Ralph et al. 1993). Individuals with a defined brood patch were classified  
106 as female and individuals with a prominent cloacal protuberance were classified as males (Ralph  
107 et al. 1993). We measured wing length and tarsus length as parameters for body condition index  
108 to the nearest 0.1 mm (Wunderle 1994). Also, we measured bird body mass as another parameter  
109 for body condition index to the nearest 0.1 g to estimate residual body condition indices. After  
110 taking measurements and extracting a small blood sample, we released all the individuals back to  
111 their habitat.

112 To diagnose infection status, we extracted 10–30  $\mu$ l of blood from the brachial vein,  
113 which we collected on filter paper and stored at 20°C. We extracted DNA from the blood  
114 samples using DNeasy Blood & Tissue Kit (Qiagen) and a nested PCR to detect parasite  
115 presence in the avian host species. We used two sets of primers, the Haem primers and the

116 MalUniv primers (S. Perkins, personal communication, 2019) to increase the probability of  
117 detection (Fallon et al. 2003, Hellgren et al. 2004). We used the diagnostic standard protocol  
118 established by Hellgren (2004). For Mal Univ, we used 10 µl of TopTaq Polymerase, 1 µl of  
119 MalUnivF primer, 1 µl of MalUnivR primer, 2 µl of coral load, 5 µl of nuclease-free water, and  
120 1 µl of DNA template per reaction (SI Article). Positive samples were detected when a band  
121 appeared in the electrophoresis gel at 500 bp and negative when no band was found (Figure 1A).  
122 We purified positive samples using the Qiagen PCR purification kit. Positive samples were  
123 sequenced using the Sanger Sequencing Service at the Sequencing and Genotyping Facility  
124 (University of PR, Rio Piedras). We analyzed the sequence using Mega X software (Kumar et al.  
125 2018) and then used the BLAST database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to determine  
126 the parasite genus. Then, we extracted the results that had 97% or more identification accuracy to  
127 identify the avian malaria parasite genus. All the infected were classified as *Haemoproteus*,  
128 *Plasmodium*, or as unclassified positive when we could not classify them based on the base pairs  
129 in the sequence. Given the limited number of *Plasmodium*-infected individuals (n=3), we  
130 restricted our analysis to *Haemoproteus* infections.

### 131 **Statistical Analysis**

132 To test if body condition decreased with infection by *Haemoproteus*, we quantified three  
133 types of body condition indices, two residual indices of body mass and a body size measurement,  
134 and a Principal Components Analysis (PCA). All the statistical analyses were conducted using  
135 the infection status results from molecular diagnostics. We used a residual body condition index  
136 by analyzing residuals of a linear relationship between natural log body mass predicted by  
137 natural log wing length, and the linear relationship between natural log body mass predicted by  
138 natural log tarsus length (SI Article). Residual indices describe body condition as a function of

139 the relationship between body length and mass (Peig & Green 2010). The residual is the  
140 difference between the observed and predicted values (Larsen & McCleary 1972). Individuals  
141 with residuals above zero are considered to have higher body condition than average and  
142 individuals with residual values below zero have poorer body condition than average. These  
143 body condition indices are commonly applied in similar studies to assess the consequences of  
144 malarial parasites on birds' health (e.g., Brock et al. 2013, Marzal et al. 2015).

145 We also tested for a decrease in body condition by avian malaria infection using a  
146 principal component analysis (PCA) which synthesizes multiple correlated variables such as  
147 mass, wing length, and tarsus length into correlated axes (Peig & Green 2010). In the PCA, the  
148 data were scaled and centered. We used the PC1 loadings as an index of body condition because  
149 PC1 explains most of the variance compared to other axes (see results section). This type of  
150 analysis is commonly applied to assess the potential negative effects of infection on hosts' health  
151 (e.g., Hatchwell et al. 2001). Still, some studies suggest caution when applying body condition  
152 indices because these are highly dependent on the body measurements used to calculate the index  
153 (Sánchez et al. 2018). To address this issue, we applied these three complementary types of body  
154 condition indices. If the results of the indices are consistent it would suggest that the result is  
155 robust. We also tested for the distributional assumption of normality of these parametric models  
156 using a Shapiro-Wilk test. To determine if body condition changed with infection status and age  
157 or sex, we used linear models with infection status and an interaction effect with age (hatch-year  
158 or juveniles-HY or after hatch-year or adults-AHY), or sex (male or female) as a predictor for  
159 body condition. Note that we conducted different models for age and sex and only on individuals  
160 with known sex or age, and infection status. We tested the need to add the mist-netting site as a  
161 random effect using a likelihood ratio test. We conducted the statistical analysis using R

162 statistical software v4.3.0 (R Core Team 2019). We used the following packages for data  
163 organization, analyses, and visualization: “ggplot2” (Wikham 2016), “dplyr” (Wikham 2023),  
164 “lme4” (Bates et al. 2015), “lmerTest” (Kuznetsova et al. 2017), “Matrix” (Bates et al. 2023),  
165 “tidyverse” (Wikham et al. 2023), “devtools” (Wikham et al. 2022), “ggbiplot” (Vu 2011),  
166 “sjPlot” (Ludecke 2023), “sjmisc” (Ludecke 2018), “sjlabelled” (Ludecke 2022), “snakecase”  
167 (Grosser 2019), “RColorBrewer” (Neuwirth 2022), “RLRsim” (Scheipl et al. 2008), “ggpubr”  
168 (Kassambara 2023), “olsrr” (Hebbali 2020) and “effects” (Fox and Weisberg 2018).

## 169 **Results**

### 170 **Body condition and infection status**

171 We captured a total of 79 Bananaquits and collected blood samples from 66 individuals.  
172 Thirteen individuals were not included in the analyses either because they escaped before the  
173 processing was completed, available blood after puncturing the brachial vein was insufficient, or  
174 because the blood coagulated in the capillary tube. Out of these, 47 were classified as adults  
175 (AHY), 13 were classified as juveniles (HY) and 2 were unidentified (U) (Table S2). From the  
176 total captured, we were able to classify 19 as male and 10 as females. A total of 18 individuals  
177 were detected through molecular diagnostics as infected by haemosporidian parasites for an  
178 overall prevalence of 27% from the sampled population. Most infections corresponded to the  
179 genus *Haemoproteus* (n=15) followed by parasites from the genus *Plasmodium* (n=3) and 3  
180 unclassified positives.

181 As expected, the linear regression model of log(weight) as a function of log(wing length)  
182 showed a clear positive relationship ( $t = 6.20$ ,  $p < 0.001$ ,  $R^2 = 0.39$ ; Table S3a). Similarly, the  
183 linear regression model of log(weight) as a function of log(tarsus length) also showed a strong

184 positive relationship ( $t = 2.98, p < 0.01, R^2 = 0.13$ ; Table S3b). Tarsus and wing length were  
185 moderately correlated ( $r = 0.32$ ).

186 On average, the body condition of infected Bananaquits was higher than uninfected ones  
187 ( $0.05 \pm 0.02$  SE) when comparing body weight relative to wing length ( $t = 2.16, p = 0.04$ ; Fig  
188 2A; Table S4a). Similarly, the body condition of infected Bananaquits was higher than  
189 uninfected ones ( $0.07 \pm 0.03$  SE) when comparing body weight relative to tarsus length ( $t = 2.59,$   
190  $p = 0.01$ ; Fig 2B; Table S4b). The linear mixed-effects model for wing length showed a singular  
191 fit and the likelihood ratio test comparing the tarsus-length model with and without a random  
192 effect for site show no clear evidence for the need for this random effect ( $LRT = 0.20, p = 0.21$ ).  
193 Therefore, we made the inferences above using fixed effects models.

194 Although the distribution of wing length deviated slightly from a normal distribution, we  
195 kept it in the PCA model after inspecting the histogram and quantile-quantile plot that showed  
196 just small deviations from normality (Fig S2–S4). The first axis, PC1, explained 62.7% of the  
197 variance, while PC2 explained 24.6%. Similar to the residual body condition index, the model  
198 predicting PCA body condition index as a function of infection status showed that infected  
199 Bananaquits had higher body condition ( $b_I = 0.96 \pm 0.40$  SE) than uninfected individuals ( $t =$   
200  $2.43, p = 0.02$ ; Figure 2C, Table S4c).

### 201 **Individual heterogeneity in body condition by infection status**

202 We did not find evidence that the effect of infection on the Bananaquit body condition  
203 varied by age ( $N = 60$ ) or sex ( $N = 29$ ). Age did not significantly contribute to variation in the  
204 body condition index either using weight relative to wing (interaction:  $t = -1.01, p = 0.32$ ; Table  
205 S5a) or tarsus length (interaction:  $t = -0.11, p = 0.91$ ; Table S5b), or using the PCA body  
206 condition index (interaction:  $t = -0.31, p = 0.76$ ; Table S5c; Fig. S5). Similarly, sex did not

207 significantly contribute to variation in the body condition index using weight relative to wing  
208 (interaction:  $t = -0.61$ ,  $p = 0.55$ ; Table S6a) or tarsus length (interaction:  $t = -0.02$ ,  $p = 0.98$ ; Table  
209 S6b), or using the PCA body condition index either (interaction:  $t = 0.51$ ,  $p = 0.62$ ; Table S6c)  
210 (Fig. S6).

## 211 **Discussion**

212 Many studies have described the negative consequences of malarial infection to naïve  
213 bird populations (LaPointe et al. 2012). Still, we know little about the consequences of infection  
214 in regions where the parasite is endemic and infections chronic. While a decrease in host  
215 survival, fecundity or other sub-lethal measures are an expected outcome of many parasitic  
216 infections (Hasik and Siepielski 2022), our results showed that infected individuals had higher  
217 body condition than uninfected ones. We found no clear evidence that these effects varied with  
218 sex or age. Therefore, our results suggest that there may be alternative underlying mechanisms  
219 that do not necessarily result in negative consequences for body condition. Three non-mutually  
220 exclusive hypotheses may explain this result: (1) metabolic syndrome that predicts higher fat  
221 storage in infected individuals, (2) host tolerance or resistance to infection, and (3) changes in  
222 foraging behavior.

223 Parasite infection can trigger immunological responses that often lead to inflammatory  
224 reactions, a decrease in muscle performance, and increased levels of carbohydrates in the blood,  
225 which is commonly known as the metabolic syndrome (Schilder & Marden 2006). Excess  
226 carbohydrates and lipids can explain why some individuals have a higher body condition (i.e.,  
227 larger mass relative to the average). In birds, accumulated lipids provide extra energy storage to  
228 survive long-distance travel (Guglielmo 2018) and in some species like the Blue Petrel is  
229 associated with improved reproductive success (Chastel et al. 1995). Still, during our sampling

230 period, our study species showed little to no body fat accumulation (per. obs.) a parameter that is  
231 highly variable depending on the Bananaquit habitat (Douglas et al. 2013, Bergstrom et al.  
232 2019). Therefore, while metabolic syndrome may explain fat accumulation in other species, there  
233 is no strong evidence supporting this hypothesis in our host-parasite system.

234         There are examples of bird diseases such as malaria and *Mycoplasma* in which  
235 populations of naïve hosts initially suffer high mortality due to parasite infection followed by a  
236 population-level decrease in these negative consequences due to resistance or tolerance traits  
237 (Sorci 2013). Tolerant individuals do not reduce or clear the infection but have mechanisms to  
238 reduce their negative effects on their survival, reproduction or other sub-lethal effects  
239 (Medzhitov et al. 2012). Hence, tolerant individuals suffer small to no parasite-induced mortality  
240 or changes in body condition. For instance, tree swallows and eastern bluebirds' nestlings show  
241 no decrease in survival when infected by the parasitic flies (*Protocalliphora sialia*) (Grab et al.  
242 2019). In rodents, it has been shown that infection by macroparasites leads to increased body  
243 condition (Jackson et al. 2014). Alternatively, resistant individuals reduce or clear parasite  
244 infection by activation of innate and adaptive immunological responses (Medzhitov et al. 2012).  
245 Contrary to tolerance, resistance can be costly to host fitness because it often results in tissue  
246 damage through the immunological response activation to eliminate the pathogen (Medzhitov et  
247 al. 2012). For instance, a study of the Seychelles warbler found that individuals' infection status  
248 was related to reactive oxygen metabolites (ROMs; van de Crommenacker et al. 2012). During  
249 the breeding stage, ROMs were significantly higher in infected individuals compared to non-  
250 infected individuals, which may indicate an immunological activation and/or the metabolic  
251 residual of the parasite infecting the individuals. Higher body condition of infected individuals  
252 compared to uninfected individuals may suggest a tolerance mechanism on the host because

253 body condition parameters show no negative effects on host physiology (Atkinson et al. 2013). It  
254 is likely that, in the Caribbean malarial parasites and the Bananaquit have co-evolved, and the  
255 parasite may have adapted to exploit resistant and/or tolerant individuals that ultimately lead to  
256 higher parasite transmission rates (Metcalf et al. 2012). Nevertheless, the mechanisms by which  
257 tolerance and resistance evolve are still not fully known. There is some evidence of genes related  
258 to immune function responding to selection pressures from vector-borne parasites (e.g.,  
259 Bonneaud et al. 2012). One related hypothesis is that we are more likely to trap chronically  
260 infected individuals because acutely infected individuals may suffer from lower mobility  
261 (Mukhin et al. 2016) and, thus, may be less likely to be trapped in our mist nets. Thus, if this  
262 parasite causes severe negative consequences to host health these individuals would die quickly  
263 or are less mobile and hence, they will have lower capture rates and be underrepresented in our  
264 samples. While our data does not allow us to differentiate between tolerance, resistance, or  
265 trapping bias, these remain key alternative hypotheses to test in future studies. For instance,  
266 previous studies have experimentally infected individuals to track their immune responses and  
267 other physiological factors through peak infection and beyond (Adelman et al. 2013).

268         As a response to offsetting the cost of infection, host species may change behavior by  
269 increasing their foraging activity which can ultimately result advantageous to the host and the  
270 parasite (Weinersmith & Earley 2016). While a recent meta-analysis showed that parasite-  
271 infected hosts consume on average 25% less food than uninfected individuals, the study showed  
272 great variability among taxa with multiple examples of the opposite pattern (Mrugala et al.  
273 2023). For instance, parasite-infected rusty crayfish consume more macrophytes and  
274 macroinvertebrates than uninfected ones likely due to increased feeding behavior boldness  
275 induced by infection (Reisinger and Lodge 2016). Also, hosts with access to more or higher

276 quality food resources would have on average better body condition and thus experience higher  
277 parasitism rates because they are optimal hosts for the parasite. Indeed, Hasik & Siepielski  
278 (2022) found that hosts with access to more prey were more heavily parasitized, though they did  
279 not relate this increased parasitism to the quality of the host for the parasite. The relationship  
280 between cost of infection and feeding behavior is likely mediated by food availability. Our study  
281 species, the Bananaquit, is generalist and highly adapted to exploit a wide variety of food  
282 resources. Therefore, the availability of a wide variety of food resources combined with a  
283 potential increase in foraging activity as a compensatory behavioral response to infection (Ots et  
284 al. 1998, Sorci 2013, Toscano et al. 2014) may also explain an increase in body condition.  
285 Natural disturbance can also have a mediating role in the effects of parasite infection on hosts'  
286 health (Sousa 1984). In September 2017, Puerto Rico suffered the impact of a strong category 4  
287 hurricane that devastated a large portion of the island causing high mortality in flora and fauna,  
288 including birds (Wunderle 2018). This high mortality event could have served as a strong  
289 selection event favoring individuals with traits related to enhanced physiological performance or  
290 immunity (e.g., Donihue et al. 2018). Therefore, if there existed a pool of weaker individuals that  
291 would have shown strong negative effects of body condition due to malarial infection, these may  
292 be underrepresented in the host population in the aftermath of the hurricane. This assumes that  
293 traits related to survival to large-scale disturbances are also related to immune response to  
294 parasites which may not necessarily be the case but still is a hypothesis that remains to be tested.

295       Previous studies have shown variable effects on individuals after natural disturbances.  
296 For instance, a study of Cerulean warblers' responses to simulated natural disturbances in the  
297 Appalachian Mountains showed that males in areas of less disturbance had better body condition  
298 compared to males in areas of heavy disturbance (Boves et al. 2013). In contrast, amphibians

299 showed a reduced risk of Bd (*Batrachochytrium dendrobatidis*) infection in areas with higher  
300 canopy openings resulting from Cyclone Yasi compared to undamaged areas (Roznik et al.  
301 2015). Therefore, hurricane disturbance may have been a factor that mediated the overall  
302 susceptibility of the bird host population.

303         Lastly, we found no clear statistical evidence of differences in infection status due to sex  
304 or age. There are strong theoretical arguments to suggest that sex and age of the infection are key  
305 determinants of quantifiable virulence traits of the host (Day 2003, Frank and Schmid-Hempel  
306 2008, Lively 2010). There is also empirical support for this theoretical idea in many host-parasite  
307 systems (e.g. Sorci and Faivre 2022, Izhar and Ben-Ami 2015, De Roode et al. 2006). There are  
308 two potential explanations for the lack of evidence in our study. Our sample size was limited  
309 when dividing the data among sex or age. Therefore, if the effect size of the effect of infection by  
310 these covariates in this system is small, the analyses may not have enough power to detect them.  
311 Alternatively, there may not necessarily be a strong difference between these traits. For instance,  
312 a recent meta-analysis on parasitism and host fitness variation also shows no clear difference by  
313 sex (Hasik and Siepielski 2022) but, they found high variability and some studies in avian  
314 malaria still have found differences in infection rates by sex (e.g., Calero-Riestra and Garcia  
315 2016). Thus, potential heterogeneities in virulence due to age or sex are still a plausible  
316 hypothesis worth further consideration.

## 317 **Conclusions**

318         Our study provides insights into the consequences of malarial infections to the most  
319 common bird in the Caribbean showing that infected individuals had higher body condition  
320 compared to uninfected individuals. Multiple hypotheses can explain the pattern in our system  
321 including tolerance in infected individuals. The tolerance hypothesis is an interesting explanation

322 for the observed patterns in our study that can be further tested by conducting controlled  
323 infection experiments.

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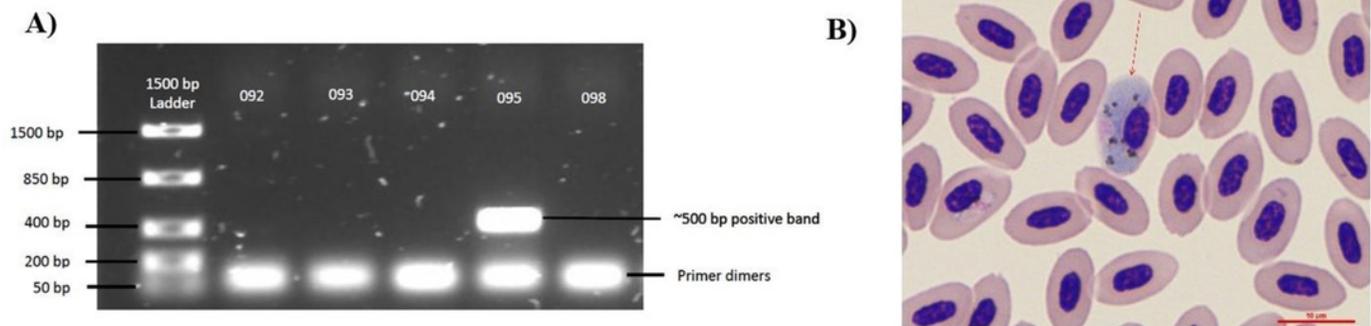
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# Figure 1

## Diagnostic techniques of *Haemoproteus* parasite infection in the Bananaquit

A) Sample 095 is positive for haemosporidian infection with a band at approximately 500 bp. Bands at 50 bp are primer dimers, a by-product of the PCR. B) Image shows a Giemsa-stained slide showing an infected erythrocyte of sample 095. Red arrow indicates an erythrocyte infected by an haemosporidian. Although we show a Giemsa-stained slide, all analyses were based on molecular diagnostics.



## Figure 2

Comparison between body condition of uninfected and infected Bananaquits by *Haemoproteus* parasites using two residual body condition indexes and a PCA body condition index

Comparison of body condition of uninfected (n=47) and infected by *Haemoproteus* (n=15) Bananaquits using a (A) wing and weight residuals index, (B) tarsus and weight residuals index and (C) PCA body condition index. The horizontal dash line at zero represents the average body condition. Individuals above the line have higher body mass than average, while individuals below the line have lower body mass than average. Jittered dots indicate individuals included in the analysis and their classification as non-infected and infected individuals. The lines indicate the 95% confidence intervals, dot indicates the point estimate of the model of the non-infected individuals and triangle indicates the point estimate of the model of the infected individuals.

