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Haemosporidian parasites prevalence associated with physical conditioning of avian species from the Brazilian Cerrado

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ABSTRACT

Blood parasites can infect myriad avian species and thereby affect the fitness and survival of their hosts. There is wide interspecific variation in parasite prevalence related to biological, ecological, and evolutionary host factors. This study aimed to determine the blood parasite prevalence in avian species from the Brazilian Cerrado and to investigate the associations among biomass, body condition, and blood parasitism. A total of 1,096 blood smears from 548 individuals (56 species) collected in four forest fragments were analyzed. Of these, 109 (19.89%) individuals from 33 species were infected: 13 (2.36%) were positive for Haemoproteus and 103 (18.76%) for Plasmodium. Among bird species, prevalence ranged from zero to 100%. There were significant positive correlations between prevalence and biomass and the body condition index. Hemosporid vectors track their hosts by carbon dioxide detection. Since large organisms emit more carbon dioxide, our results suggest that larger birds may be more susceptible to hemosporid vectors. Additionally, species with higher body condition indices can be more tolerant to parasites, possibly because they have more energy reserves. This study showed that species with higher biomass and body condition indices were associated with higher blood parasite prevalence, a finding that suggests these factors are efficient predictors to explain the interspecific variations.

Keywords: avian malaria, wild birds, host-parasite relationship

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1 INTRODUCTION

Parasitism is an ecological relationship that affects the dynamics and evolution of animal populations. It exerts important selective forces such as predation and of competition (WATSON, 2013). Protozoan hemosporids the genus Haemoproteus and Plasmodium are considered model for organisms understanding evolutionist and ecological theories (ATKINSON; VAN RIPPER, 1991), because they have a wide geographic distribution (CLARK et al., 2014) and attack several types of vertebrate hosts (VALKIUNAS, 2005). These parasites are considered threats to species conservation, especially when introduced into populations not adapted to them (ATKINSON; LA POINTE, 2009). In this sense, they can promote population decline and extinction and may affect the structure of the host communities (VAN RIPPER III et al., 1986; ATKINSON; LA POINTE, 2009).

In birds, hemosporids can occur in several species (VALKIUNAS, 2005); however, the impacts are difficult to estimate in natural populations, and especially in areas where they are common and hosts are adapted (ISAKSSON *et al.*, 2013). Despite this fact, many Haemoproteus and Plasmodium species are responsible for acute and/or chronic infections in domestic and wild birds (ZIEGYTE; VALKIUNAS, 2014). Such infections can be pathogenic, causing host deaths (VANSTREELS *et al.*, 2014; DINHOPL *et al.*, 2015), or may reduce physical and reproductive aptitudes (ASGHAR *et al.*, 2011; KNOWLES *et al.*, 2010) by modulating various factors, including neural development (SPENCER *et al.*, 2005), vocalization, and sexual selection (HAMILTON; ZUK, 1982; BALENGER; ZUK, 2014).

These parasites are transmitted by hematophagous insects (Diptera: Culicidae, Ceratopogonidae, Hippoboscidae, Simuliidae) and present a complex development cycle, which includes asexual reproduction in bird tissues and sexual reproduction in dipteran gut (VALIKUNAS, 2005). Vectors have great abundance and diversity in tropical environments (NUNN *et al.*, 2005), where large hemosporid diversity is observed (LACORTE *et al.*, 2013).

There is a large variation in hemosporid prevalence among avian species in a community. Interspecific differences have been attributed to biological, ecological, and evolutionary host factors, as well as aspects related to the vectors' ecology (HAMILTON; ZUK, 1982; READ, 1991; SEBAIO *et al.*, 2010; FECCHIO *et al.*, 2011). Hemosporid prevalence variations can be related to how host species deal with infection, namely controlling or maintaining it. Additionally, it can be related to factors that cause differential exposure to the vectors (FECCHIO *et al.*, 2011).

Heavier birds may be more susceptible to vectors, since larger organisms can emit greater amounts of carbon dioxide, which is the main chemical compound used by the vectors to track their hosts (LEHANE, 2005). Birds with higher biomasses are usually related to higher body condition indices (BAESSE, 2015). These indices are measurements of the organisms' fitness and may indicate the capacity to store energy (SCHULTEDE-HOSTEDDE *et al.*, 2005). Parasitic infections can negatively affect the bird body condition because of the high energy cost in controlling infections (MARZAL *et al.*, 2013; GETHINGS *et al.*, 2016). However, in some host species, the infection does not affect their body condition, a finding that suggests some species are more tolerant to parasites than others (MOLNÁR *et al.*, 2013; MAIA *et al.*, 2014; MEGÍA-PALMA *et al.*, 2016).

This study aimed to determine the blood parasite prevalence in avian species from the Brazilian Cerrado and to investigate the interspecific prevalence variations using bird biomass and body condition. We hypothesized that species with higher biomass and body condition indices are related to higher hemosporid prevalence. The studied species are described in table 1.

2 MATERIAL AND METHODS

2.1 Study Site

The study was performed in four seasonal semideciduous forest areas in the Triângulo Mineiro region, Minas Gerais State, Brazil. The region is located in the Cerrado biome, but it is highly impacted, with more than 70% of the area occupied by agriculture and livestock (BRITO; PRUDENTE, 2005). The climate of the region is the Aw

type according to the Köppen classification, characterized by marked seasonality, with rainy and dry seasons. Annual rainfall is around 1,500 mm, and the average temperature is 22°C (ROSA *et al.*, 1991). The forest fragments studied were situated in: 1. Mata da Água Fria Farm (18°29′50″S; 48°23′03″O): in the Araguari municipality, with 200 ha; 2. RPPN Galheiro (19°14′S; 47°08′O): in the Perdizes municipality, with 260 ha; 3. Glória Experimental Farm (Federal University of Uberlândia) (18°57′03″S; 48°12′22″O) and 4. São José Farm (18°51′25″S; 48°13′53″O): both in the Uberlândia municipality, with 30 and 20 ha, respectively.

2.2 Capture of birds

A total of 548 individual birds from 56 species and 21 families were captured from June 2013 to December 2015. Birds were captured using 20-25 mist nets (12 x 3 m) exposed in tracks from 06:00 to 17:00; they were checked at 30-min intervals. Weight and tarsus length measurements were performed for all captured birds by using hand dynamometers and a digital caliper, respectively. Individuals were identified according to Sigrist (2009) and Gwynne *et al.* (2010) and marked with a metal ring provided by the Research Center for Wild Bird Conservation in Brazil (CEMAVE/ICMBio – Authorization: 3730 – Registry: 359076). Nomenclature and systematic order were determined according to the Brazilian Committee of Ornithological Records (PIACENTINI *et al.*, 2015).

2.3 Preparation and analysis of blood smears

Blood samples (5.0 µl) were collected from the tarsal-metatarsal veins using syringes with sterile and disposable needles (8 mm x 0.3 mm) (SISBIO/ICMBio – Authorization: 44901) (CEUA/UFU – Authorization: 001/12). Duplicate blood smears were prepared, air-dried, and fixed in absolute methanol. After staining with Giemsa's solution (5%), the slides were examined microscopically (BRAGA *et al.*, 2010). Approximately 200 fields were screened using a 100x objective lens and immersion oil (GODFREY *et al.*, 1987). Hemosporid identifications were performed according to Valkiunas's descriptions (2005).

2.4. Statistical analyzes

To estimate the individual bird's body condition, the relative mass index (RMI) was calculated by a simple linear regression between logarithmic values of the right tarsus and biomass (SCHULTEDE-HOSTEDDE *et al.*, 2005). Regression residual values were used for RMI (Supplementary file 1). To verify the relationship between hemosporid prevalence and avian biomass or body condition, Pearson correlations were used. The premise of normality was met by logarithmically transforming the data. The analyses were made only for species that presented a minimum number of 5 individuals, conducted at a significance level of 5% (ZAR, 1999), and performed with SYSTAT 10.2 software (WILKINSON, 2002).

3 RESULTS

A total of 1,096 blood smears were analyzed in this study. The overall hemosporid prevalence was 19.89%. For *Haemoproteus* spp. and *Plasmodium* spp., 13 (2.37%) and 103 (18.8%) birds were positive, respectively. Co-infection with both parasite genera occurred in seven individuals. The prevalence among species ranged from zero to 100%. A total of 23 species did not present any infected individuals, whereas in 5 species all the individuals were infected. Of the 56 analyzed species, 33 (59%) were positive for Plasmodium spp.. Of these, 6 (10.7%) were also infected by Haemoproteus spp. (Table 1).

Table 1 - Avian species examined and infected according to the parasites genera and the variables used in the statistical analyzes. ¹: Species that were first recorded as hosts of hemosporids. ²: Species that presented individuals with co-infection by the two genera of parasites

Таха	Individuals:		Parasites:		Variables:	
	Examined	Infected (%)	Haemoproteus	Plasmodium	Biomass (g)	RMI
Columbidae						
Claravis pretiosa	2	0	0	0		
Caprimulgidae						

Таха	Individuals:		Parasites:		Variables:	
	Examined	Infected (%)	Haemoproteus	Plasmodium	Biomass (g)	RMI
Nyctidromus albicollis	1	0	0	0		
Bucconidae						
Nonnula rubecula	4	0	0	0		
Monasa nigrifrons²	5	5 (100%)	4	5	67.50	0.546
Picidae						
Picumnus albosquamatus	2	1 (50%)	0	1		
Veniliornis passerinus	1	0	0	0		
Thamnophilidae						
Dysithamnus mentalis²	6	1 (16.6%)	1	1	12.60	-0.151
Herpsilochmus longirostris	2	0	0	0		
Thamnophilus doliatus	1	1 (100%)	0	1		
Thamnophilus pelzelni	5	1 (20%)	0	1	21.0	0.009
Thamnophilus caerulescens	2	0	0	0		
Taraba major¹	1	1 (100%)	0	1		
Pyriglena leucoptera	3	0	0	0		
Conopophagidae						
Conopophaga lineata	5	1 (20%)	0	1	22.50	-0.089
Dendrocolaptidae						
Sittasomus griseicapillus	2	0	0	0		
Xiphorhynchus fuscus	1	0	0	0		
Lepidocolaptes angustirostris	1	0	0	0		
Dendrocolaptidae						
Dendrocolaptes platyrostris	1	0	0	0		
Furnariidae						
Clibanornis rectirostris	3	1 (33.3%)	0	1		

Таха	Individuals:		Parasites:		Variables:	
	Examined	Infected (%)	Haemoproteus	Plasmodium	Biomass (g)	RMI
Automolus leucophthalmus	1	1 (100%)	0	1		
Syndactyla dimidiata	1	0	0	0		
Synallaxis scutata	7	2 (28.5%)	0	2	14.0	-0.112
Pipridae						
Neopelma pallescens¹	12	3 (25%)	0	3	18.66	0.141
Pipra fasciicauda	40	4 (10%)	1	3	15.50	0.062
Antilophia galeata	123	30 (24.3%)	3	27	22.0	0.001
Onychorhynchidae						
Myiobius barbatus	1	0	0	0		
Tityridae						
Schiffornis virescens ¹	5	1 (20%)	0	1	27.50	0.080
Platyrinchidae						
Platyrinchus mystaceus	5	1 (20%)	0	1	9.0	-0.137
Rhynchocyclidae						
Mionectes rufiventris	4	0	0	0		
Leptopogon amaurocephalus	24	6 (25%)	0	6	11.53	-0.060
Corythopis delalandi ¹	17	1 (5.8%)	0	1	13.70	-0.223
Rhynchocyclidae						
Tolmomyias sulphurescens	19	4 (21%)	0	4	16.60	-0.002
Tyrannidae						
Elaenia parvirostris ¹	14	2 (14.2%)	0	2	16.75	0.038
Elaenia mesoleuca	7	4 (57.1%)	0	4	17.50	0.099
Myiopagis viridicata	1	1 (100%)	0	1		
Myiarchus tyrannulus	1	0	0	0		
Sirystes sibilator	2	0	0	0		
Casiornis rufus	4	1 (25%)	0	1		
Cnemotriccus fuscatus	4	0	0	0		

Таха	Individuals:		Parasites:		Variables:	
	Examined	Infected (%)	Haemoproteus	Plasmodium	Biomass (g)	RMI
Lathrotriccus euleri	5	2 (40%)	0	2	12.50	-0.038
Vireonidae						
Cyclarhis gujanensis	4	1(25%)	0	1		
Hirundinidae Stelgidopteryx ruficollis	1	0	0	0		
Troglodytidae Cantorchilus leucotis	3	0	0	0		
Turdidae						
Turdus leucomelas²	19	5 (26.3%)	1	5	63.0	0.243
Turdus rufiventris	3	1 (33.3%)	0	1		
Turdus albicollis	1	0	0	0		
Passerellidae						
Arremon flavirostris¹	12	3 (25%)	0	3	30.77	0.085
Parulidae						
Basileuterus culicivorus	48	3 (6.25%)	0	3	10.73	-0.223
Myiothlypis flaveola	47	7 (14.8%)	0	7	13.43	-0.212
Myiothlypis leucophrys ¹	13	2 (15.3%)	0	2	18.80	-0.138
Thraupidae						
Tangara cayana	4	2 (50%)	2	0		
Eucometis penicillata²	27	4 (14.8%)	1	4	27.44	0.118
Tersina viridis	1	0	0	0		
Coereba flaveola	2	0	0	0		
Saltator maximus	11	3 (27.2%)	0	3	44.57	0.244
Saltator similis	7	3 (42.8%)	0	3	45.28	0.208
Total	548	109 (19.89%)	13 (2.37%)	103 (18.80%)		

For statistical analysis, 483 individuals from 24 species were used (only species with 5 or more individuals). There was a significant positive correlation between hemosporid prevalence and the average species biomass (r = 0.492, df = 22, p =

0.014), a finding that indicates heavier avian species were more susceptible to hemosporid infection (Fig. 1). There was also a significant positive correlation between prevalence and the average species RMI values (r = 0.679, df = 22, p = 0.001), data that demonstrate infection probability may be higher in species with higher body condition indices (Fig. 2).

Fig. 1 -Scatter plot that demonstrates the positive correlation between hemosporid prevalence and the average biomass of the avian species

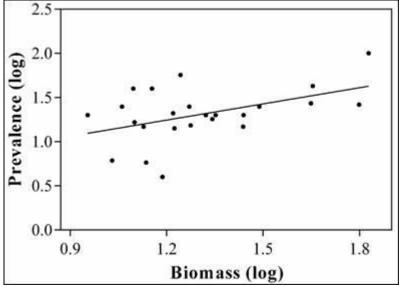
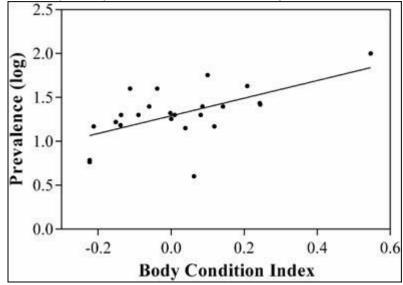


Fig. 2 - Scatter plot that demonstrates the positive correlation found between hemosporid prevalence and the body condition index of the avian species



4 DISCUSSION

This study demonstrated the presence of hemosporids in wild birds from the Brazilian Cerrado. The recorded prevalence (19.89%) was comparable to that reported in earlier studies conducted in birds from the same biome (21% and 24.4%) but higher than that found in social birds (10.7%) (FECCHIO *et al.* 2013; BELO *et al.*, 2011; FECCHIO *et al.*, 2011). To our knowledge, the present study is the first report of hemosporids in *Taraba major*, *Neopelma pallescens*, *Schiffornis virescens*, *Corythopis delalandi*, *Elaenia parvirostris*, *Arremon flavirostris*, and *Myiothlypis leucophrys*. New hemosporid hosts were previously found in Brazil (FECCHIO *et al.*, 2007; SEBAIO *et al.*, 2012; LACORTE *et al.*, 2013), a fact that indicates although the Brazilian avifauna is one of the most diverse worldwide (PIACENTINI *et al.*, 2015), basic information about several species is still unknown.

The prevalence of hemosporids among avian species ranged from zero to 100%. The marked variation in prevalence seems to be common in bird communities, since this pattern was previously reported by several authors (FECCHIO *et al.*, 2007, 2011, 2013; BELO *et al.*, 2011; LEITE *et al.*, 2013). Natural factors can be responsible for this amplitude, since parasite prevalence in a community depends on a complex interaction between biotic and abiotic factors, including biological, ecological, and behavioral host aspects (BELO *et al.*, 2011; FECCHIO *et al.*, 2011, 2013) as well as habitat, vegetation, and climate characteristics (LACORTE *et al.*, 2013; FERREIRA JUNIOR *et al.*, 2017).

The relationship between hemosporid prevalence and average species biomass was positive and significant, data that corroborate the hypothesis that larger species are more susceptible to infection. In Cerrado bird communities, this association was previously tested by Fecchio *et al.* (2011), who found no relationship, and by Lobato (2012), who verified that heavier birds are more infected. This relationship can be attributed to biological and behavioral characteristics of vectors and birds. Hematophagous insects locate their hosts visually, recognizing color and body shape. They also use olfactory methods, through the detection of carbon dioxide and lactic

acid (MARQUARDT, 2005). Thus, heavier birds may be more susceptible to be located by the vectors, since larger animals release more volatile compounds and can provide a larger surface area for foraging activity by the vectors (SCHEUERLEIN; RICKLEFS, 2004; LEHANE, 2005).

In the present study, all individuals of *Monasa nigrifrons* (black-fronted nunbird), the species with the highest recorded biomass, were positive for hemosporids. This species lives in groups, uses "sit-and-wait" foraging behavior, and nests in cavities on the ground or in gullies (SICK, 1997; SIGRIST, 2009). These characteristics may improve the location of the animals by vectors. According to Fecchio *et al.* (2011), it is expected that more carbon dioxide is emitted in groups than by solitary individuals, and such compounds can accumulate inside cavities, increasing the odor source for the vectors.

Body condition analysis allows estimating the individual's capacity to store energy resources and survive adverse situations. Indices with negative values indicate worse body condition when compared to positive values (SCHULTEDE-HOSTEDDE *et al.*, 2005). In a Cerrado bird community, Baesse (2015) verified that heavier species exhibit higher body condition indices. Therefore, as in the current study where the heavier species were related to higher parasites prevalence, it was expected that such a relationship would also be found for species with higher body conditions.

There was a positive relationship between infection and body condition. This relationship was previously reported by other studies, a fact that suggests organisms with higher energy reserves are more tolerant to parasites because they provide more resources for parasite reproduction and development (MOLNÁR *et al.*, 2013; MAIA *et al.*, 2014; Megía-Palma *et al.*, 2016). However, there are reports of negative relationships (MARZAL *et al.*, 2013; GETHINGS *et al.*, 2016), which indicates commitment to host fitness, since the energy used in the host's physiological and reproductive processes is redirected to the immune system to control parasite proliferation (SORCI; FAIVE, 2009).

There is probably a trade-off between host resistance and tolerance to parasites (CORNET *et al.*, 2013; SORCI, 2013). The trade-off is understood as the costs and benefits of a particular biological strategy. Resistance refers to the ability of hosts

to control infection, but at a high cost, while tolerance indicates the ability to maintain parasites at the lowest cost (RÅBERG *et al.*, 2009; AYRES; SCHNEIDER, 2012; MEDZHITOV *et al.*, 2012). In an experimental study, Cornet *et al.* (2013) found that the birds more resistant to parasitic infections are also less tolerant. According to Sorci (2013), there is a large interspecific variation in a bird's propensity to be resistant or tolerant to parasites. It is likely that biological differences between species are one of the predictors in this variation. Heavier species with higher body condition indices may be more tolerant, as evidenced in the current study.

5 CONCLUSION

This study found a large variation in the hemosporid (*Plasmodium* and *Haemoproteus*) prevalence among the examined avian species. The biomass and body condition indices were efficient to explain these variations. Species with higher biomass and body condition indices were related to higher hemosporid prevalence. Therefore, this study can be considered important for understanding the host-parasite relationship and useful for bird conservation programs.

REFERENCES

Asghar M, Hasselquist D, Bensch S. Are chronic avian haemosporidian infections costly in wild birds?. Journal of Avian Biology. 2011;42:530-537.

Atkinson CT, La Pointe, DA. Introduced avian diseases, climate change, and the future of Hawaiian honeycreepers. Journal of Avian Medicine and Surgery. 2009;23:53-63.

Atkinson CT, Van Ripper III C. Pathogenicity and epizootilogy of avian haematozoa: *Plasmodium, Leucocytozoon* and *Haemoproteus*. In: LOYE JR, ZUK M, editors. Bird parasite interactions. Oxford: Oxford University Press; 1991. p. 19-48.

Ayres JS, Schneider DS. Tolerance of Infections. Annual Review of Immunology. 2012;30:271-294.

Baesse CQ. Aves como biomonitores de qualidade ambiental em fragmentos florestais do Cerrado. [dissertation]. Uberlândia: Instituto de Biologia/UFU; 2015. 114 p.

Balenger SL, Zuk M. Testing the Hamilton–Zuk hypothesis: past, present, and future. Integrative and Comparative Biology, 2014;54:601-613.

Braga EM, Belo NO, Pinheiro RT. Técnicas para estudo de hemoparasitos em aves. In: MATTER SV *et al.*, editors. Ornitologia e Conservação: Ciência Aplicada, Técnicas de Pesquisa e Levantamento. Rio de Janeiro: Editora Technical Books; 2010. p. 395-412.

Belo NO, Pinheiro RT, Reis ES, Ricklefs RE, Braga EM. Prevalence and lineage diversity of avian haemosporidians from three distinct Cerrado habitats in Brazil. Plos One. 2011;6:1-8.

Brito JLS, Prudente TD. Mapeamento do uso da terra e cobertura vegetal do município de Uberlândia – MG, utilizando imagens CCD/CBERS 2. Caminhos de Geografia. 2005;13:144-153.

Clark NJ, Clegg SM, Lima MR. A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from molecular data. International Journal for Parasitology. 2014;44:329-338.

Cornet S, Bichet C, Larcombe S, Faivre B, Sorci G. Impact of host nutritional status on infection dynamics and parasite virulence in a bird-malaria system. Journal of Animal Ecology. 2013;10:1-10.

Dinhopl N, Nedorost N, Mostegl MM, Weissenbacher-Lang C, Weissenböck H. In situ hybridization and sequence analysis reveal an association of Plasmodium spp. with mortalities in wild passerine birds in Austria. Parasitology Research. 2015;114:1455-62.

Fecchio A, Marini MÂ, Braga ÉM. Baixa prevalência de hemoparasitos em aves silvestres no Cerrado do Brasil Central. Neotropical Biology and Conservation. 2007;2:127-135.

Fecchio A, Lima MR, Silveira P, Braga ÉM, Marini MÂ. High prevalence of blood parasites in social birds from a neotropical savanna in Brazil. Emu. 2011;111:132-138.

Fecchio A, Lima MR, Svensson-Coelho M, Marini MÂ, Ricklefs RE. Structure and organization of an avian haemosporidian assemblage in a Neotropical savanna in Brazil. Parasitology. 2013;140:181-192.

Ferreira Junior FC, Rodrigues RA, Ellis VA, Leite LO, Borges MA, Braga EM. Habitat modification and seasonality influence avian haemosporidian parasite distributions in southeastern Brazil. Plos One. 2017;12:1-18.

Gethings OJ, Sage RB, Morgan ER, Leather SR. Body condition is negatively associated with infection with Syngamus trachea in the ring-necked pheasant (*Phasianus colchicus*). Veterinary Parasitology. 2016;228:1-5.

Godfrey RD, Fredynich, AM, Pence DB. Quantification of hematozoan in blood smears. Journal of Wildlife Disease. 1987;23:558-565.

Gwynne JA, Ridgely RS, Tudor G, Argel M. Aves do Brasil: Pantanal e Cerrado. Belo Horizonte: Editora Horizonte; 2010.

Hamilton WD, Zuk M. Heritable true fitness and bright birds: a role for parasites? Science. 1982;218:384-387.

Isaksson C, Sepil I, Baramidze V, Sheldon BC. Explaining variance of avian malaria infection in the wild: the importance of host density, habitat, individual life-history and oxidative stress. BMC Ecology. 2013;13:1-11.

Knowles SCL, Palinauskas V, Sheldon BC. Chronic malaria infections increase family inequalities and reduce parental fitness: experimental evidence from a wild bird population. Journal of Evolution Biology. 2010;23:557-569.

Lacorte GA, Felix GMF, Pinheiro RRB, Chaves AV, Almeida-Neto G. Exploring the diversity and distribution of neotropical avian malaria parasites – a molecular survey from southeast Brazil. Plos one. 2013;8:1-9.

Lehane M. The Biology of Blood-Sucking in Insects. New York: Cambridge University Press, 2005.

Leite YFC, Pinheiro RT, Braga EM. Prevalência de hemosporídeos em três localidades do estado do Tocantins, Brasil. Ornithologia. 2013;6:1-13.

Lobato DNC. Efeitos das alterações ambientais sobre a saúde de aves silvestres utilizando hemoparasitos como indicadores. [thesis]. Belo Horizonte: Instituto de Ciências Biológicas/UFMG; 2012. 120p.

Maia JP, Harris DJ, Carranza S, Gómez-Díaz EA. Comparison of multiple methods for estimating parasitemia of haemogregarine hemoparasites (Apicomplexa: Adeleorina) and its applications for studying infection in natural populations. Plos One. 2014;9:1-13.

Marquardt WC. Biology of disease vectors. San Diego: Elsevier Academic Press; 2005

Marzal A, Asghar M, Rodríguez L, Reviriego M, Hermosell IG, Balbontín J, Garcia-Longoria L, Lope F, Bensch S. Co-infections by malaria parasites decrease feather growth but not feather quality in house martin. Journal of Avian Biology. 2013;44:437-444.

Medzhitov R, Schneider DS, Soares MP. Disease tolerance as a defense strategy. Science. 2012; 335:936-941.

Megía-Palma R, Martínez X, Merino S. A structural colour ornament correlates positively with parasite load and body condition in an insular lizard species. The Science of Nature. 2016;103:1-10.

Molnár O, Bajer K, Mészáros B, Török J, Herczeg G. Negative correlation between nuptial throat colour and blood parasite load in male European green lizards supports the Hamilton-Zuk hypothesis. Naturwissenschaften. 2013;100:551-558.

Nunn CL, Altizer SM, Sechrest W, Cunningham A.A. Latitudinal gradients of parasite species richness in primates. Diversity and Distributions. 2005;11:249-256.

Piacentini VQ, Aleixo A, Agne CE, Mauricio GN, Pacheco JF, Bravo GA, *et al.* Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee. Revista Brasileira de Ornitologia. 2015;23:91-298.

Råberg L, Graham AL, Read AF. Decomposing health: tolerance and resistance to parasites in animals. Philosophical Transactions of the Royal Society: Biological Sciences. 2009364:37-49.

Read AF. Passerine Polygyny: A Role for Parasites?. The American Naturalist. 1991;138:434-459.

Rosa R, Lima SC, Assunção WL. Abordagem preliminar das condições climáticas de Uberlândia (MG). Sociedade ; Natureza. 1991;3:91-108.

Scheuerlein A, Ricklefs RE. Prevalence of blood parasites in European passerine birds. Proceedings of the Royal Society of London. 2004; 271: 1363–1370.

Schultede-Hostedde AI, Zinner B, Millar JS, Hickling GJ. Restitution of mass-size residuals: validating body condition indices. Ecology. 2005;86:155-163.

Sebaio F, Braga EM, Branquinho F, Naninca LT, Marini MA. Blood parasites in Brazilian Atlantic Forest birds: effects of fragment size and habitat dependency. Bird Conservation International. 2010;20:432-439.

Sebaio F, Braga ÉM, Branquinho F, Fecchio A, Marini MÂ. Blood parasites in passerine birds from the Brazilian Atlantic Forest. Revista Brasileira de Parasitologia Veterinária. 2012;21:7-15.

Sick H. Ornitologia brasileira: uma introdução. Rio de Janeiro: Editora Nova Fronteira; 1997.

Sigrist T. Aves do Brasil: uma visão artística. São Paulo: Editora Leitura Dinâmica; 2009.

Sorci G, Faivre B. Inflammation and oxidative stress in vertebrate host-parasite systems. Philosophical Transactions of the Royal Society B: Biological Sciences. 2009;364:71-83.

Sorci G. Immunity, resistance and tolerance in bird-parasite interactions. Parasite Immunology. 2013;35:350-361.

Spencer KA, Buchanan KL, Leitner S. Parasites affect song complexity and neural development in a songbird. Proceedings of the Royal Society of London B: Biological Sciences. 2005;272:2037-2043.

Valkiunas G. Avian malaria parasites and other haemosporidians. Boca Raton: CRC Press; 2005.

Van Riper III C, Van Riper SG, Goff ML. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs. 1986;56:327-344.

Vanstreels RET, Kolesnikovas CKM, Sandri S, Silveira P, Belo NO, Ferreira Junior, FC, *et al*. Outbreak of avian malaria associated to multiple species of *Plasmodium* in magellanic penguins undergoing rehabilitation in southern Brazil. Plos One. 2014;9:1-11.

Watson MJ. What drives population-level effects of parasites? Meta-analysis meets life-history. International Journal for Parasitology: Parasites and Wildlife. 2013;2:190-196.

Wilkinson L. SYSTAT: The System for Statistics. Chicago: SYSTAT Inc.; 2002.

Zar JH. Biostatistical Analysis. Rio de Janeiro: Prentice-Hall; 1999.

Žiegytė R, Valkiūnas G. Recent advances in vector studies of avian haemosporidian parasites. Ekologija. 2014;60:73-83.