



## Prevalence of avian haemosporidian parasites and their host fidelity in the central Philippine islands

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### ABSTRACT

We examined the prevalence and host fidelity of avian haemosporidian parasites belonging to the genera *Haemoproteus*, *Leucocytozoon* and *Plasmodium* in the central Philippine islands by sampling 23 bird families (42 species). Using species-specific PCR assays of the mitochondrial cytochrome *b* gene (471 base pairs, bp), we detected infections in 91 of the 215 screened individuals (42%). We also discriminated between single and multiple infections. Thirty-one infected individuals harbored a single *Haemoproteus* lineage (14%), 18 a single *Leucocytozoon* lineage (8%) and 12 a single *Plasmodium* lineage (6%). Of the 215 screened birds, 30 (14%) presented different types of multiple infections. Intrageneric mixed infections were generally more common (18 *Haemoproteus*/*Haemoproteus*, 3 *Leucocytozoon*/*Leucocytozoon*, and 1 *Plasmodium*/*Plasmodium*) than intergeneric mixed infections (7 *Haemoproteus*/*Leucocytozoon* and 1 *Haemoproteus*/*Leucocytozoon*/*Plasmodium*). We recovered 81 unique haemosporidian mitochondrial haplotypes. These clustered in three strongly supported monophyletic clades that correspond to the three haemosporidian genera. Related lineages of *Haemoproteus* and *Leucocytozoon* were more likely to derive from the same host family than predicted by chance; however, this was not the case for *Plasmodium*. These results indicate that switches between host families are more likely to occur in *Plasmodium*. We conclude that *Haemoproteus* has undergone a recent diversification across well-supported host-family specific clades, while *Leucocytozoon* shows a longer association with its host(s). This study supports previous evidence of a higher prevalence and stronger host-family specificity of *Haemoproteus* and *Leucocytozoon* compared to *Plasmodium*.

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### 1. Introduction

Avian haemosporidian parasites comprise a diverse group of vector-transmitted parasites that infect red blood cells and other organs within their bird host [1]. In this study, we consider three of the four genera belonging to this group, *Haemoproteus*, *Leucocytozoon* and *Plasmodium*. These parasites reproduce asexually in various tissues of the vertebrate host before invading and circulating with the blood. *Plasmodium* undergoes an additional asexual multiplication phase in the peripheral blood. Thus, *Plasmodium* infections are thought to be more dangerous [2]. Sexual reproduction of these parasites occurs in a dipteran vector a few minutes after the dipteran has taken a blood meal. Therefore, mated gametes normally come from a single host. The primary vectors for *Haemoproteus* parasites are biting midges of the genus *Culicoides* (Diptera: Ceratopogonidae) and louse-flies (Diptera: Hippoboscidae). *Leucocytozoon* is transmitted by blackflies (Diptera: Simuliidae) and *Plasmodium* by mosquitoes belonging to the genera *Culex*, *Aedes*, *Culiseta*, *Anopheles*, *Mansonia* and *Aedeomyia* [1–6].

Molecular studies of *Haemoproteus* and *Plasmodium* lineages in the Australo-Papuan region demonstrate strong host-family specificity in *Haemoproteus* [7]. In contrast, several lineages of *Plasmodium* infect multiple host families, suggesting extensive host-switching between different host families [7]. *Leucocytozoon*, which is sister to the *Haemoproteus*/*Plasmodium* clade [8], has received comparatively less attention but also shows host-family specificity [9]. The ability of some parasites to invade new hosts can have devastating effects especially in extremely vulnerable contexts such as remote oceanic islands. The case of Hawaiian honeycreepers is illustrative; these birds have experienced a drastic decline due to the introduction of *Plasmodium relictum* [10]. Therefore, it is important to study the fidelity of avian haemosporidia in the wild.

The Philippine archipelago comprises some 7100 islands, most of which are volcanic in origin. Its complex geological evolution is well known [11–14] and has greatly impacted the evolution of its fauna, resulting in a wealth of biological diversity with one of the highest degrees of endemism in the world [15]. The Philippine archipelago is considered one of the most species-rich biodiversity hot spots on Earth [16]. Thus, the archipelago provides an attractive system for characterizing the diversity of haemosporidian parasite species and for evaluating their degree of fidelity to a variety of hosts.

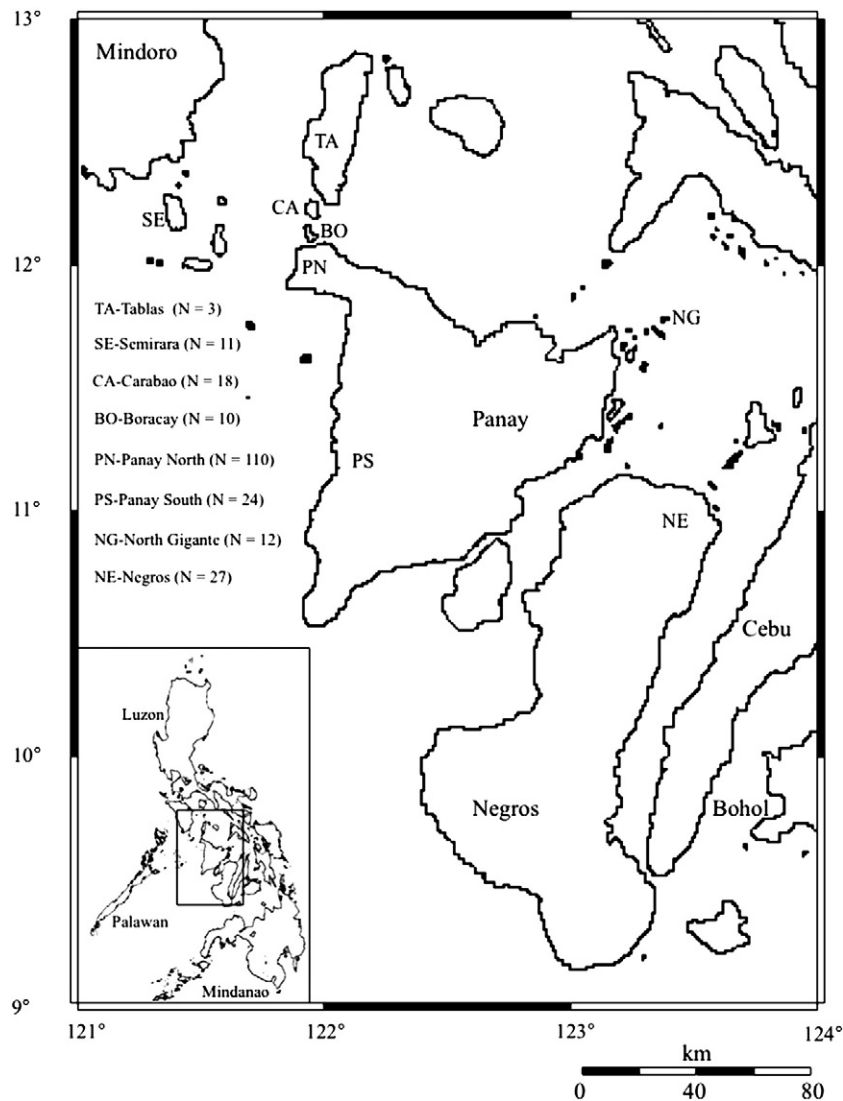
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Multiple infections increase competition among parasite genotypes, favoring rapid growth to achieve greater relative success within the host. Such overexploitation of a host may cause virulence that can result in the death of both species (the parasite and the host), or the host can develop a resistance to excessive parasitic infections. Here, we investigate the occurrence of *Haemoproteus* spp., *Leucocytozoon* spp. and *Plasmodium* spp. in 42 bird species belonging to 23 families from different field sites across the central Philippine islands (Tablas, N = 3; Semirara, N = 11; Carabao, N = 18; Boracay, N = 10; Panay, N = 134, North Gigante, N = 12 and Negros, N = 27) using selective screening by Polymerase Chain Reaction (PCR). We designed this study with three aims: i) to test whether the occurrence of these three avian parasites is evenly distributed across taxonomically diverse host species, ii) to discriminate between single and mixed infections and iii) to detect possible patterns of co-speciation in the chosen host–parasite system. We used molecular methods to determine whether birds were infected by homospecific (i.e., different lineages of the same parasite) or heterospecific (i.e., co-occurrence of different parasites) infections.

## 2. Materials and methods

### 2.1. Sampling

The birds were caught with mist nets from seven islands in the Philippine archipelago: Tablas, Semirara, Carabao, Boracay, North Gigantes, Negros and Panay (Fig. 1). The samples from Boracay, Panay, and Negros were collected in March 2004 while the remnant islands were surveyed in March 2006. A small amount of blood (approximately 10  $\mu$ L) was taken by puncturing the ulnar (wing) vein with a small needle. The blood was collected in a micro-hematocrit tube. All birds were ringed and released alive. We collected 215 blood samples from 42 species of birds belonging to 23 bird families (Appendix A). The great majority of samples came from Panay (134 birds belonging to 21 bird families). We collected 27, 18, 12, 11, 10, and 3 blood samples from: Negros, Carabao, North Gigantes, Semirara, Boracay, and Tablas, respectively. Because of the proximity of these islands and also because of the disequilibrium in the number of samples collected in different localities, we did not focus on geographic aspects in this study.



**Fig. 1.** Location of sampling sites in the Philippines. The bottom left inlet shows the entire archipelago and the area included in the present study. Names of the major islands are also given. Abbreviations are population codes; sample sizes (N) are given in parentheses. Agpulos, Tablas Is., TA (N = 3); Bala Bago, Semirara Is., SE (N = 11); Combot, Carabao Is., CA (N = 18); Yepak, Boracay Is. BO (N = 10); Sibaliw, Panay Is. (North), PN (N = 110); Hamtang, Panay Is. (South), PS (N = 24); Granada, North Gigante Is., NG (N = 12); and Patag, Negros Is., NE (N = 27).

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