



# Avian malaria infection intensity influences mosquito feeding patterns

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## ABSTRACT

Pathogen-induced host phenotypic changes are widespread phenomena that can dramatically influence host–vector interactions. Enhanced vector attraction to infected hosts has been reported in a variety of host–pathogen systems, and has given rise to the parasite manipulation hypothesis whereby pathogens may adaptively modify host phenotypes to increase transmission from host to host. However, host phenotypic changes do not always favour the transmission of pathogens, as random host choice, reduced host attractiveness and even host avoidance after infection have also been reported. Thus, the effects of hosts' parasitic infections on vector feeding behaviour and on the likelihood of parasite transmission remain unclear. Here, we experimentally tested how host infection status and infection intensity with avian *Plasmodium* affect mosquito feeding patterns in house sparrows (*Passer domesticus*). In separate experiments, mosquitoes were allowed to bite pairs containing (i) one infected and one uninfected bird and (ii) two infected birds, one of which treated with the antimalarial drug, primaquine. We found that mosquitoes fed randomly when exposed to both infected and uninfected birds. However, when mosquitoes were exposed only to infected individuals, they preferred to bite the non-treated birds. These results suggest that the malarial parasite load rather than the infection itself plays a key role in mosquito attraction. Our findings partially support the parasite manipulation hypothesis, which probably operates via a reduction in defensive behaviour, and highlights the importance of considering parasite load in studies on host–vector–pathogen interactions.

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## 1. Introduction

Pathogen-induced phenotypic changes in host morphology, behaviour and physiology may greatly affect interactions between hosts and insect vectors, and may in turn have an impact on the transmission dynamics of vector-borne pathogens (Hurd, 2003; Libersat et al., 2009; Poulin, 2010; Lafferty and Kuris, 2012). Despite not having a full understanding of its underlying mechanisms, the parasite manipulation hypothesis (Poulin, 1995; Hurd, 2003) has received increasing attention during the last decade (e.g. Lefèvre and Thomas, 2008; Lefèvre et al., 2009). This hypothesis proposes that pathogens manipulate a host's phenotype to increase host–vector contact rates, thereby enhancing both the probability of pathogen acquisition and the transmission to a new host (Lefèvre et al., 2006; Lefèvre and Thomas, 2008; Mauck et al., 2010, 2012). Indeed, the enhanced attractiveness of infected

hosts to vectors has been reported in plants (Eigenbrode et al., 2002; Shapiro et al., 2012), invertebrates (Stafford et al., 2011) and vertebrates (O'Shea et al., 2002; Cornet et al., 2013a; De Moraes et al., 2014) including humans (Lacroix et al., 2005; Batista et al., 2014).

Malaria parasites of the genus *Plasmodium* are vector-borne pathogens that require the bite of a competent mosquito to spread from an infected to a new host (Valkiunas, 2005). A number of studies have reported vector preference for mammalian hosts already infected by malaria parasites. For example, in humans, children harbouring *Plasmodium falciparum* parasites in transmissible stages (i.e. gametocytes) were more attractive to mosquitoes (measured as a reaction to odours) than those harbouring parasites in non-transmissible stages (i.e. trophozoites) or uninfected children (Lacroix et al., 2005). Similarly, Day and Edman (1983) found that mosquitoes fed almost exclusively on malaria-infected mice when both infected and uninfected individuals were made available. However, whether host infection affects vector feeding behaviour remains an open question since contrasting results were also reported. For instance, mosquitoes preferred to feed on bats

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infected with the mildest stages of the malaria-like parasite *Polychromophilus murinus* (Witsenburg et al., 2014) or even preferred to feed on uninfected hosts to the detriment of their infected counterparts (Daugherty et al., 2011).

Avian malaria parasites have recently been used to test the parasite manipulation hypothesis since they may alter host behaviour (e.g. reduced activity, Cauchard et al., 2016) and physiology (e.g. anaemia and enlargement of the liver and spleen, Valkiūnas, 2005), which could potentially affect mosquito attraction. Nonetheless, contradictory trends have been also reported and, for instance, Cornet et al. (2013a) found that birds chronically infected by *Plasmodium relictum* were bitten more frequently by the avian malaria vector *Culex pipiens* than their uninfected or acutely infected counterparts. This finding would support the parasite manipulation hypothesis, as this behaviour would increase the fitness of parasites (transmission success) (Poulin, 1995). On the other hand, Lalubin et al. (2012) reported that *Cx. pipiens* were more attracted to uninfected birds than to *Plasmodium*-infected birds, a finding that cannot be explained by parasitic manipulation but rather by the hypothesis of vector adaptive avoidance (Hart, 1990; Martínez-de la Puente et al., 2009; Lalubin et al., 2012). This latter hypothesis is based on the costs induced by parasites in their vectors, such as decreased fecundity (Vézilier et al., 2012) and survival (Ferguson and Read, 2002; Lalubin et al., 2012). However, Cornet et al. (2013a) used birds infected in the laboratory that were deprived of movement, which may not reflect the situation that occurs in the field. The study by Lalubin et al. (2012) suffers from the technical problem when using olfactometers, i.e. the lack of physical interaction between birds and mosquitoes (e.g. feeding attempts and hosts' defence). Therefore, the actual effects of parasitic infection on vectors' feeding patterns remain to be clarified.

Here, we conducted two separate experiments to determine the effects of avian *Plasmodium* infection on the feeding behaviour of the avian malaria vector *Cx. pipiens*. Firstly, we exposed naturally infected and uninfected house sparrows (*Passer domesticus*) to mosquitoes to assess the effect of birds' infection status on mosquito biting rates. Secondly, we assessed the effect of host parasite load on the probability of mosquito bites by treating half of the *Plasmodium*-infected birds (hereafter, 'treated' in this experiment) with an antimalarial drug and then exposing both infected (hereafter, 'control' in this experiment) and treated birds to mosquito bites. In both cases, the pairs of birds representing dual conditions of malaria infection (i.e. infected versus uninfected or control versus treated) were exposed simultaneously to mosquitoes to simulate a common situation of making choices as faced by mosquitoes in the field. In addition, birds were allowed to move freely in their cages to avoid hampering anti-mosquito behaviour that could greatly affect the feeding success of mosquitoes (Darbro and Harrington, 2007). According to the parasite manipulation hypothesis, we predicted that *Plasmodium*-infected control (non-treated) birds would be bitten more often than uninfected and treated individuals, respectively, as parasite-induced changes (e.g. hosts' odours, anti-mosquito behaviours) would facilitate mosquito bites (Day and Edman, 1983; De Moraes et al., 2014). Alternatively, and according to the adaptive avoidance hypothesis, we predicted that mosquitoes would bite infected control birds less often than uninfected and treated birds, since mosquitoes may adaptively select uninfected birds or those with less intense infections to avoid the costs of infection.

## 2. Materials and methods

### 2.1. Mosquito and bird collection and rearing

Mosquito larvae were collected in the Cañada de los Pájaros nature reserve (37°14'03" N, 6°07'50" W, Seville, Spain) during the

summer of 2014 and then transported to the laboratory, where they were supplied with shrimp food (Mikrozell 20 ml/22 g; Dohse Aquaristik GmbH & Co. KG, D-53501, Gelsdorf, Germany) and maintained under controlled conditions (65–70% relative humidity (RH),  $27 \pm 1$  °C and a light (L): dark (D) cycle of 12:12 h). Emerged mosquitoes were anaesthetised with diethyl ether (Lipnick, 1991), sexed and identified following Schaffner et al. (2001). Female *Cx. pipiens* were maintained in insect rearing cages (BugDorm-43030F,  $32.5 \times 32.5 \times 32.5$  cm) with ad libitum access to 1% sucrose solution. Mosquitoes were deprived of sucrose solution 24 h before the experiment took place and henceforth only had access to water.

In July 2014, 78 juvenile house sparrows were captured using mist nets in Huelva province (southern Spain). Birds were ringed upon capture and their body mass and wing length were measured using a digital scale (Pesola-MS500) and a 30 cm end-stop ruler, respectively. A blood sample was obtained for further molecular analyses (see Section 2.3). Birds were transferred to the Unit of Animal Experimentation at Estación Biológica de Doñana-Consejo Superior de Investigaciones Científicas (EBD-CSIC), Spain where they were maintained in pairs in cages ( $58.5 \times 25 \times 36$  cm) within a vector-free room programmed with a photoperiod cycle of 12:12 h L:D at  $22 \pm 1$  °C. Birds were housed for 1 week before the start of the experiments and had ad libitum access to fresh water and a standard mixed diet for seed and insect-eater birds (KIKI; GZM S.L., Alicante, Spain). Birds were released at their capture site 2–5 days after the completion of the experiments. All experimental procedures were approved by the CSIC Ethics Committee and Animal Health authorities as per Spanish legislation (CEBA-EBD-12-40).

### 2.2. Experimental procedure

Before performing the experiments, birds were molecularly sexed (see Section 2.3) and their infection status with blood parasites (i.e. *Plasmodium*, *Haemoproteus* and *Leucocytozoon*) was determined using primer pairs HaemNF1/HaemNR3 and HaemF/HaemR2 following Hellgren et al. (2004). Their infection status with blood parasites was determined again after completion of the experiments. The presence of amplicons was verified in 1.8% agarose gels. Positive amplifications were sequenced using the Big-Dye technology (Applied Biosystems, USA) or by the MacroGen sequencing service (MacroGen Inc., The Netherlands). Sequences were edited using the software Sequencher™ v 4.9 (Gene Codes Corp. © 1991–2009, Ann Arbor, MI, USA 48108) and assigned to parasite lineages/morphospecies after comparisons with sequences in GenBank (National Center for Biotechnology Information, (NCBI), USA). Birds infected with *Haemoproteus* or *Leucocytozoon* were not included in this study. In the first experiment, 20 pairs of birds consisting of a *Plasmodium*-infected (10 males and 10 females) and an uninfected bird (10 males and 10 females) were exposed to unfed female *Cx. pipiens* (mean number = 172, range = 156–183). In this experiment, a *Plasmodium*-infected bird was also co-infected with *Haemoproteus* as determined by sequencing of blood after the completion of the experiment. Besides this co-infected bird, 15 individuals were infected with the lineages Rinshi-1 (*P. relictum*), three infected with Rinshi-7 (*P. relictum*), and one bird co-infected with both Rinshi-1 and Donana07 (*Plasmodium* spp.). Each pair contained one male and one female bird, with one infected and one uninfected individual. Eight to 18 day old female mosquitoes were used in all experiments to reduce the potential effect of mosquito age on host location capacity (Bohbot et al., 2013). In the second experiment carried out 15 days after completing the first experiment, only *Plasmodium*-infected birds were used; 16 infected birds (including the above-mentioned co-infected bird) from the first experiment were

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