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ARE MALARIA-INFECTED BIRDS MORE ATTRACTIVE TO MOSQUITO VECTORS?

¿SON LAS AVES INFECTADAS POR MALARIA MÁS ATRACTIVAS PARA LOS MOSQUITOS VECTORES?

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Summary.—According to the host manipulation hypothesis, parasites modify the hosts' phenotype to maximise their transmission success. Avian malaria parasites and related haemosporidians are vector-borne parasites infecting birds worldwide. Recent studies have reported a greater attraction of mosquitoes

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to infected birds, supporting the host manipulation hypothesis. Changes in the composition of the uropygial gland secretion of birds associated with infections have been proposed as the potential mechanisms explaining this pattern. Here we critically review the published information on the host manipulation hypothesis in the context of avian malaria infections. We focus this article on the suggested role of the secretions of the uropygial gland and bird odours as mosquito attractants. The role of uropygial gland secretions as attractants of mosquitoes was poorly supported by available literature. In contrast, changes in the odour profile of infected birds or a reduction in the anti-mosquito behaviour of infected individuals may explain the parasite-mediated effects on mosquito attraction and biting rates. Finally, we propose future research approaches to identify the role of parasite infections on the interaction between birds and insect vectors.—Martínez-de la Puente, J., Díez-Fernández, A., Soriguer, R.C., Rambozzi, L., Peano, A., Meneguz, P.G. & Figuerola, J. (2021). Are malaria-infected birds more attractive to mosquito vectors? *Ardeola*, 68: 205-218.

Key words: *Culicoides, Haemoproteus*, *Leucocytozoon*, mosquitoes, parasites, *Plasmodium*.

RESUMEN.—Según la hipótesis de manipulación del hospedador, los parásitos modifican el fenotipo del hospedador para maximizar su éxito de transmisión. Los parásitos de la malaria aviar y los hemosporidios relacionados son parásitos transmitidos por vectores que infectan a las aves de todo el mundo. Estudios recientes han encontrado apoyo para una mayor atracción de mosquitos hacia las aves infectadas, lo que respalda la hipótesis de la manipulación del hospedador. Cambios en la composición de la secreción de la glándula uropigial de las aves asociados a las infecciones se han propuesto como un posible mecanismo para explicar este patrón. Aquí, revisamos críticamente la información publicada sobre la hipótesis de la manipulación del hospedador en el contexto de las infecciones por malaria aviar. Centramos este artículo en el papel sugerido de las secreciones de la glándula uropigial y los olores de las aves como atrayentes de mosquitos. El papel de las secreciones de la glándula uropigial como atrayentes de mosquitos tuvo poco apoyo en la literatura. Por el contrario, los cambios en el perfil de olor de las aves infectadas o una reducción del comportamiento antimosquitos de los individuos infectados pueden explicar los efectos mediados por parásitos en la atracción de mosquitos y las tasas de picadura. Finalmente, proponemos perspectivas de investigación futuras para identificar el papel de las infecciones parasitarias en la interacción entre las aves y los insectos vectores.—Martínez-de la Puente, J., Díez-Fernández, A., Soriguer, R.C., Rambozzi, L., Peano, A., Meneguz, P.G. y Figuerola, J. (2021). ¿Son las aves infectadas por malaria más atractivas para los mosquitos vectores? *Ardeola*, 68: 205-218.

Palabras clave: *Culicoides, Haemoproteus*, *Leucocytozoon*, mosquitos, parasitos, *Plasmodium*.

INTRODUCTION

The host manipulation hypothesis argues that parasites are able to modify host phenotypes to enhance parasite transmission success. This hypothesis has been largely tested using different study models considering a diversity of parasites infecting invertebrate and vertebrate hosts, including birds (reviewed in Heil, 2016).

Avian malaria parasites belonging to the genus *Plasmodium* are widespread parasites of the phylum Apicomplexa, commonly found infecting birds in every continent except Antarctica (Valkiūnas, 2005). Avian *Plasmodium* is phylogenetically related to other common parasites also infecting birds such as the malaria-like parasites of the genera *Haemoproteus* and *Leucocytozoon*. These three parasite genera are transmitted from an infected bird to a new susceptible host by different dipteran insect vectors. Species of *Plasmodium* are transmitted by mosquitoes (Family Culicidae) (Santiago-Alarcón *et al*., 2012). Hippoboscids (Hippoboscidae) and biting midges (Ceratopogonidae) are considered the main vectors of *Haemoproteus* species while parasites of

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the genus *Leucocytozoon* are mainly transmitted by blackflies (Simuliidae) (Valkiūnas, 2005; Santiago-Alarcón *et al*., 2012). However, some exceptions have been reported to this general pattern: for example, *Leucocytozoon caulleryi* is transmitted by biting midges (*Culicoides* spp.) instead of blackflies (Valkiūnas, 2005).

Avian malaria and malaria-like parasites are important selective agents affecting the ecology, evolution and conservation of their bird hosts. These parasites are known to induce deleterious effects on bird health (Marzal *et al*., 2008), breeding success (Merino *et al*., 2000) and survival (Marzal *et al*., 2008; Martínez-de la Puente *et al*., 2010; Asghar *et al*., 2015), acting as drivers of some avian population declines (Van Riper III *et al*., 1986; Niebuhr *et al*., 2016; Dadam *et al*., 2019). Thus, factors increasing contact rates between infected and susceptible birds and insect vectors could have important consequences for individual fitness and population dynamics and should be studied. According to the host manipulation hypothesis, vector-borne avian malaria parasites may improve their transmission success by increasing the feeding rate of competent vectors on infected birds. These effects could be driven by an increase in the attractiveness of infected birds to vectors. Birds protect themselves from mosquito bites by moving their legs, wings and heads to drive away mosquitoes (Darbro & Harrington, 2007). An increase in the biting rate of mosquitoes on vertebrate hosts could be also favoured by a reduction in the anti-mosquito behaviour of infected individuals. These possibilities have been broadly studied using multidisciplinary approaches during the last years providing contrasting results. Thus, the ability of these parasites to modify bird phenotypes, and thereby the mechanisms used by parasites to increase their transmission, remain unclear. In this article, we critically review the published information on the bird manipulation hypothesis in the context of avian malaria infections and focus on the suggested role of the secretions of the uropygial gland and body odour of birds as attractants of mosquitoes. In addition, we propose future research possibilities to test the host manipulation hypothesis, considering novel approaches based on the study of the role of bird odours in determining mosquito-bird-parasite interactions.

Vector attraction towards malaria-infected birds

According to the host manipulation hypothesis, parasites manipulate the phenotype of the infected individuals to increase parasite transmission (Heil, 2016). In the case of avian malaria, the host manipulation hypothesis proposes that parasites may manipulate infected birds to attract more mosquitoes than are attracted by uninfected ones. Researchers have used different approaches to compare the attraction of mosquitoes towards infected and uninfected birds. For instance, Lalubin *et al*. (2012) used a dual-choice olfactometer to compare the attraction of *Culex pipiens* towards wild Great Tits *Parus major* that were uninfected or naturally infected by *Plasmodium* parasites. Contrary to the predictions of the host manipulation hypothesis, these authors found that mosquitoes were more attracted to uninfected birds than by infected ones. However, the use of naturally infected birds does not exclude the possibility that vectors were attracted to uninfected individuals because of some other physiological difference that could decrease their initial probability of infection. In a field experiment, a lower number of biting midges were captured in nest-boxes of Blue Tit *Cyanistes caeruleus* pairs medicated with the antimalarial drug primaquine than in nests of control pairs (Tomás *et al*., 2008). These results support the host avoidance hypothesis which

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argues that insect vectors may develop different mechanisms to reduce their contact rates with infected vertebrates, because the parasites may also have deleterious effects on the vectors, especially after these bite birds with high intensities of infection (Anderson *et al*., 2000; Valkiūnas *et al*., 2014; Bukauskaitė *et al*., 2016; Gutiérrez-López *et al*., 2019a).

Dipteran insect vectors use different cues, such as chemical and visual stimuli, to locate their hosts (Lehane, 2005). It has been proposed that insect vectors are attracted by the secretion of the uropygial or preen gland. This secretion contains different compounds including alcohols, aldehydes and waxes that could be used by mosquitoes to locate their hosts. If parasites modify the composition of the secretion of the uropygial gland, this could be a potential mechanism to increase the attractiveness of infected birds to mosquitoes. In this case, it could be expected that i) parasites modify the composition of the uropygial gland secretion of birds and ii) mosquitoes are more attracted to the secretions of parasite-infected birds than uninfected ones.

Grieves *et al*. (2018) found that malaria infection (*Plasmodium* sp. lineage 99% similar to P-SOSP 2) modified the wax ester composition of the secretions of the uropygial gland of Song Sparrows *Melospiza melodia*. However, it is unclear if the volatile and semivolatile compounds of the uropygial gland secretions of birds derived from these wax esters. By contrast, Díez-Fernández *et al*. (2020b) did not find differences in the composition of the volatile fraction of uropygial gland secretions of House Sparrows *Passer domesticus* whether uninfected or infected by *Plasmodium* parasites. Birds in this latter study were naturally infected by *Plasmodium* parasites corresponding to four different genetic lineages (SGS1, GRW11, COLL1 and PADOM01). These contrasting results suggest that differences in the effect of parasites on the composition of the secretions of the uropygial gland may vary between bird species, parasite lineages and the fractions of the secretion analysed (volatile fraction *vs* wax esters).

Different authors have analysed the attraction of mosquitoes towards the secretion of the uropygial gland. Russell and Hunter (2005) found that CDC traps located 5m above ground level and supplemented with uropygial gland secretions captured more *Cx. pipiens* and *Cx. restuans* mosquitoes than unbaited traps. However, this attractant effect of the bird secretions was not found when traps were located 1.5m above ground level. The use of dual choice olfactometers found no attraction toward uropygial gland secretions by *Cx. pipiens* or *Aedes caspius* mosquitoes (Díez-Fernández *et al*., 2020a). In addition, while live adult House Sparrows attracted more *Cx. pipiens* mosquitoes than nestlings, a similar degree of attraction was observed when mosquitoes were exposed to uropygial gland secretions of these bird age classes (Garvin *et al*., 2018). No differences were also reported by Martínez-de la Puente *et al*. (2011) when comparing the attraction of biting midges to miniature UV-CDC traps whether or not these were baited with the uropygial gland secretions of pigeons. Moreover, biting midges were absent in unoccupied nest-boxes baited with the uropygial gland secretions of Blue Tits *Cyanistes caeruleus* (Martínez-de la Puente *et al*., 2011). Thus, in spite of the findings of Russell and Hunter (2005), the role of uropygial gland secretions as attractants of mosquitoes is poorly supported.

Díez-Fernández *et al*. (2020b) found differences in the attraction of *Cx. pipiens* to stimuli from birds uninfected and infected by *Plasmodium* parasites, with a higher attraction of mosquitoes to the body odours but not the uropygial gland secretions of infected House Sparrows. In this study, the authors used birds naturally infected by avian

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Plasmodium parasites. Therefore, it was not possible to distinguish if the observed differences were the cause or the consequence of parasite infections. In spite of this limitation, these results support the absence of a direct impact of infection by avian *Plasmodium* parasites on mosquito attraction to birds by their uropygial gland secretions. While the odour of infected birds attracts more mosquitoes, these results raise new questions on the potential causes of changes in bird odour profiles and the nature of the substances involved in the higher attraction for mosquitoes associated with parasitic infections. Previous studies on other malaria models support a link between host odours, parasitic infections and vector attraction (De Moraes *et al*., 2014; Schaber *et al*., 2018). For example, *Plasmodium falciparum* infections are associated with the presence of terpenes (alpha-pinene and 3-carene) in the breath of children that may increase the attraction of mosquitoes towards infected individuals (Schaber *et al*., 2018). Some components of bird odours, such as nonanal, have been identified as attractants of mosquitoes (Syed & Leal, 2009). The odour profile of birds may be determined, at least in part, by the surface microbiota on the skin and feathers (Krause *et al*., 2018). Bird mi-

TABLE 1

Different compounds of bird uropygial gland secretions potentially affecting bird-mosquito interactions. Some of these components may act as attractants or repellents of insect vectors as well as possibly having deleterious effects on arthropods and other organisms potentially affecting the mosquito-host interactions.
[Diferentes compuestos de las secreciones de la glándula uropigial de las aves que podría afectar las interacciones ave-mosquito. Algunos de estos compuestos podrían actuar como atrayentes o repelentes de insectos vectores así como podrían tener efectos deletéreos sobre los artrópodos y otros organismos, afectando potencialmente las interacciones mosquito-hospedador.]

Compound	Potential function	Reference	Examples of bird species with the compound	Reference
Ketone				
2-Tridecanone	Insecticide	Williams *et al*. (1980)	Gray Catbird *Dumetella carolinensis*	Shaw *et al*. (2011)
			Dark-eyed Junco *Junco hyemalis*	Whittaker *et al*. (2018) Soini *et al*. (2007)
			Spotless Starling *Sturnus unicolor*	Amo *et al*. (2012)
			White-throated Sparrow *Zonotrichia albicollis*	Tuttle *et al*. (2014)
Aldehydes				
Nonanal	Mosquito attractant	Syed & Leal (2009)	Dark-eyed Junco *Junco hyemalis*	Soini *et al*. (2007)

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TABLE 1 (cont.)

Compound	Potential function	Reference	Examples of bird species with the compound	Reference
Carboxilic acids				
Dodecanoic acid (= lauric acid)	Antimicrobial	Huang *et al*. (2011)	Bohemian Waxwing *Bombycilla garrulus*	Zhang *et al*. (2013)
			Japanese Waxwing *Bombycilla japonica*	
			Gray Catbird *Dumetella carolinensis*	Shaw *et al*. (2011)
			Dark-eyed Junco *Junco hyemalis*	Whittaker *et al*. (2018) Soini *et al*. (2007)
			White-throated Sparrow *Zonotrichia albicollis*	Tuttle *et al*. (2014)
Tetradecanoic acid	Mosquito repellent and larvicidal	Sivakumar *et al*. (2011)	Bohemian Waxwing *Bombycilla garrulus*	Zhang *et al*. (2013)
			Japanese Waxwing *Bombycilla japonica*	
			Gray Catbird *Dumetella carolinensis*	Shaw *et al*. (2011)
			Dark-eyed Junco *Junco hyemalis*	Whittaker *et al*. (2018)
Hexadecanoic acid*	Mosquito repellent and adulticide	Anuradha & Yogananth (2015)	Bohemian Waxwing *Bombycilla garrulus*	Zhang *et al*. (2013)
			Japanese Waxwing *Bombycilla japonica*	
			Dark-eyed Junco *Junco hyemalis*	Whittaker *et al*. (2018)
			Budgerigar *Melopsittacus undulatus*	Zhang *et al*. (2010)
Aromatic compound				
Phenol	Nematicide	Gu *et al*. (2007)	Green Woodhoopoe *Phoeniculus purpureus*	Burger *et al*. (2004)
			Eurasian Hoopoe *Upupa epops*	Martín-Vivaldi *et al*. (2009)

* contained in *Halophila ovalis* extracts in combination with other compounds.

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crobiota may be altered by properties of some components of the uropygial gland secretions (Table 1) potentially affecting birds's odours and their interaction with vectors (see Magallanes *et al*., 2016). In addition, uropygial gland secretions may protect plumage by forming a physical barrier to microbes (Reneerkens *et al*., 2008). Blood parasite infections may reduce the antimicrobial activity of uropygial gland secretions (Magallanes *et al*., 2016), which could explain, at least in part, the differential mosquito attraction to the odours of *Plasmodium* spp. infected birds and of uninfected ones. New studies are necessary to test these possibilities.

Mosquito biting rates and avian malaria infections

After reaching a host bird, mosquitoes and other dipteran insect vectors feed on blood by biting unfeathered parts such as tarsi or eye-rings. Different methods have been used to identify the susceptibility of avian malaria-infected and uninfected birds to mosquito attacks by exposing birds individually (Gutiérrez-López *et al*., 2019b) or in pairs (Cornet *et al*., 2013a, 2013b; Yan *et al*., 2018) to insect bites under controlled conditions in the laboratory (Figure 1). In the latter case, molecular techniques were used to assess the individual origin of the blood meals present in the abdomens of vectors. It was found that more *Cx. pipiens* mosquitoes bit Canaries *Serinus canaria* that were experimentally infected with *P. relictum* lineage SGS1 than bit uninfected birds. However, such differences were only significant during the chronic phase of infection. Similarly, Yan *et al*. (2018) performed two experiments to test whether the infection status or the intensity of infection affect the number of bites that each bird received from mosquitoes. Although the rates at which infected and uninfected individuals were bitten did not differ in this study, they found that mosquitoes fed at a greater rate on birds infected by *Plasmodium* parasites (controls) than they did on those infected individuals with an experimentally reduced parasite load. However, contrary to the case of Cornet *et al*. (2013a), birds tested by Yan *et al*. (2018) were free to respond to mosquitoes attempting to bite them and, consequently, the results were influenced both by the extent of attraction of mosquitoes and by the susceptibility of the birds to mosquito bites. This is especially important because fewer mosquitoes may be able to complete a blood meal on birds that display more active anti-mosquito behaviour, such as preening or scratching. Overall, these studies support the hypothesis that prior infection with avian *Plasmodium* parasites affects the attraction of *Cx. pipiens* mosquitoes to bird hosts, with the phase of infection and/or parasite load in the host likely eliciting a stronger response by mosquitoes. Thus, the infection characteristics of the host need to be considered in epidemiological studies of avian malaria parasites because these variables can explain part of the heterogeneity in attacks by vectors (Cornet *et al*., 2013a; Yan *et al*., 2018), the success of parasite development in mosquitoes (Pigeault *et al*., 2015) and the impact of parasite infections on the insect vectors (Bukauskaitė *et al*., 2016; Gutiérrez-López *et al*., 2019a).

Interestingly, the infection by *Plasmodium* parasites may also affect the behaviour of vectors (Rossignol *et al*., 1986; Choumet *et al*., 2012). Parasites may increase their transmission in different ways including an increase in the frequency or duration of the contacts between insect vectors and susceptible hosts (Heil, 2016). *Aedes aegypti* mosquitoes carrying *P. gallinaceum* sporozoites ingested a lower blood volume during a blood meal and were more likely to probe for a second meal than uninfected mosquitoes (Koella, 2002). Further experiments have revealed that mosquitoes carrying the infec-

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tive forms of avian malaria parasites need more time to complete a blood meal than uninfected mosquitoes and are more likely to take reduced blood meals (Rossignol *et al*., 1986). Thus, mosquitoes may bite several times to obtain a complete blood meal. This change in mosquito behaviour could be explained by changes in the regulation/activity of the enzyme apyrase, which is involved in the anticoagulation of mosquito saliva (Rossignol *et al*., 1984; Thiévent *et al*., 2019).

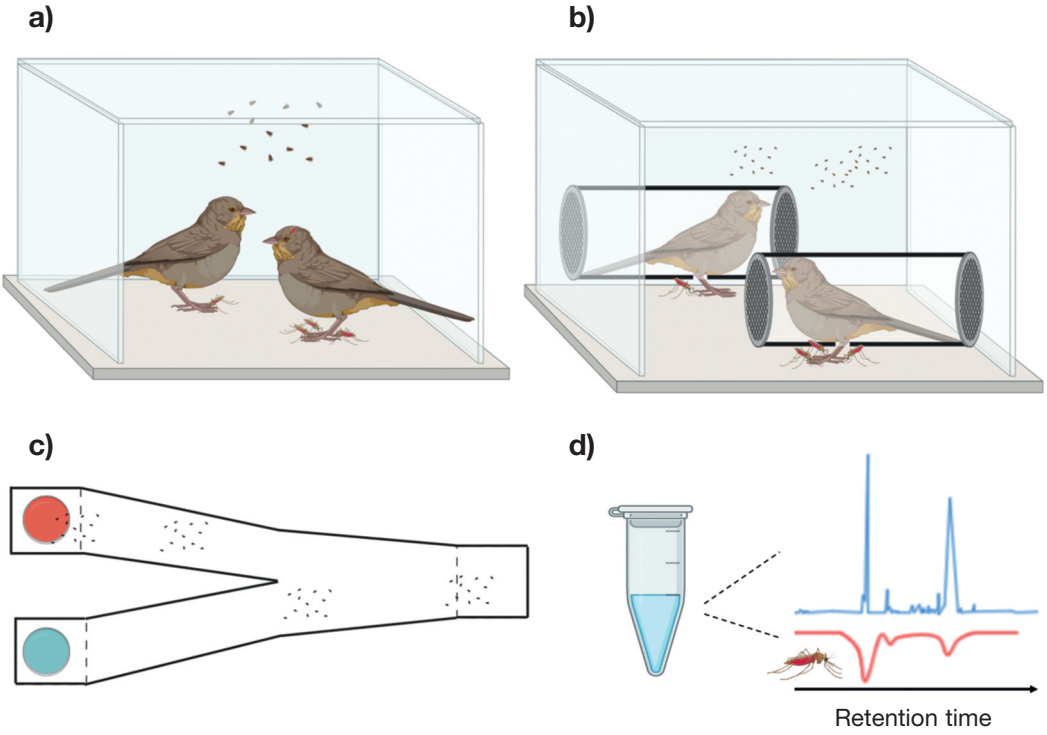


FIG. 1.—Different approaches used to test the host manipulation hypothesis using birds and avian malaria parasites, including the use of free-moving (a) and immobilised birds (b) exposed in pairs (e.g. infected vs un-infected birds; heavily- vs lightly infected birds). c) Dual choice olfactometers have been used to test the attraction of mosquitoes to bird stimuli (e.g. secretions of the uropygial gland or body odours). d) Gas chromatography coupled with electroantennographic detection can be used to identify the compounds of birds' uropygial gland secretions or body odours and the response of mosquitoes to these compounds according to the host infection status. Figure created with BioRender.com.
[Diferentes aproximaciones usadas para testar la hipótesis de la manipulación del hospedador usando aves y parásitos de la malaria aviar, incluyendo el uso de aves con libertad de movimiento (a) e inmovilizadas (b) expuestas en parejas (p.e. aves infectada vs *no infectada; aves con una alta* vs *baja intensidad de infección). c) Olfatómetros de doble elección han sido usados para comprobar la atracción de los mosquitos a los estímulos de las aves (p.e. secreciones de la glándula uropigial u olores de las aves). d) Cromatografía de gases acoplada con la detección de electroantenogramas puede ser usada para identificar los compuestos de las secreciones de la glándula uropigial u olor corporal de las aves y la respuesta de los mosquitos frente a estos compuestos de acuerdo con el estado de infección de las aves. La figura fue creada con BioRender.com.]*

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Concluding remarks and future study possibilities

The host manipulation hypothesis has mainly been tested considering a handful of bird-parasite-vector assemblages and virtually no study has analysed the *Haemoproteus*/biting midge-hippoboscid nor *Leucocytozoon*/black fly systems. This is especially significant considering the large number of vector species potentially involved in the transmission of these parasites, which may affect the observed patterns of host-parasite-vector associations. In addition, more than 4,000 lineages of avian malaria and malaria-like parasites have been recorded to date (according to Malavi; Bensch *et al*., 2009). These lineages may present different virulences in their bird hosts (Ilgūnas *et al*., 2019a; 2019b) that may determine different degrees of vector attraction to infected individuals. However, the relationship between parasite virulence and vector attractivity has never been tested. Interspecific differences in the intensity of anti-mosquito behaviours (Darbro & Harrington, 2007) and bird body size and coloration (Yan *et al*., 2017) may determine the differential susceptibility of each bird species to vector attacks, with some species being preferred by mosquitoes while others are bitten less often than expected from their densities in the wild (Simpson, 2009; Rizzoli *et al*., 2015). The different vector species involved in the transmission of avian malaria and malaria-like parasites may use different cues to locate their bird hosts, potentially explaining discrepancies between studies.

It is also important to standardise the methods used in studies considering such aspects as the use of immobilised/free moving exposed birds and the number of insect vectors and/or hosts included in each experimental trial. For example, studies using immobilised birds may provide information on the importance of such cues as odour or temperature in host selection by mosquitoes, while using free-moving birds allows the impact of anti-mosquito behaviour on mosquito feeding success to be considered. In addition, anti-mosquito behaviours may be more frequent/intense in trials using a greater number of mosquitoes (Darbro & Harrington, 2007). The number of birds exposed to mosquitoes may also affect the relative attractiveness of a specific host with respect to those available nearby, finally affecting the feeding patterns of insect vectors. For example, in cavity nesting species, nestlings are exposed to insect attacks in close proximity and consequently the bites received by an individual will be the outcome of the relative attractiveness to mosquitoes of this individual in relation to its nest mates (Christe *et al*., 1998). However, most studies conducted until now have been performed by exposing birds to vector bites individually or in pairs. In addition, different host-related factors including prior experience of mosquito attacks, haematocrit, body temperature or sex classes could be also important determinants of the susceptibility of individuals to vector attacks. Again, in the case of bird sex, experiments analysing its impact on mosquito feeding preferences have given mixed results, because differences have only been reported in some bird/mosquito species combinations (Gutiérrez-López *et al*., 2019b; Cozzarolo *et al*., 2019; Burkett-Cadena *et al*., 2014). For example, Gutiérrez-López *et al*. (2019b) exposed House Sparrows *Passer domesticus* and Jackdaws *Corvus monedula* to the bites of two mosquito species, *Cx. pipiens* and *Ae. caspius*. In this study, *Ae. caspius* showed a higher biting rate on female Jackdaws than on males. However, there was no significant difference in the biting rates of either mosquito on House Sparrows nor in the case of Jackdaws exposed to *Cx. pipiens*. Nevertheless, mixed infections by different parasite genera of avian malaria and malaria-like parasites are frequently found in wild birds

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(Marzal *et al*., 2008; Martínez *et al*., 2009; Ciloglu *et al*., 2019). In addition, infections by other vector-borne blood parasite taxa, such as microfilariae, *Trypanosoma* spp., *Hepatozoon* spp. and *Lankesterella*-like parasites, are common in birds (Merino *et al*., 1997; Merino *et al*., 2007). These mixed infections could affect the attractiveness of avian hosts to insect vectors in different ways as these parasites are transmitted by different vector groups. In addition, parasites could induce strong deleterious effects on non-competent insects, potentially favouring an avoidance rather than an attractive effect. For instance, *Haemoproteus* parasites, which are transmitted by biting midges (*Culicoides* spp.), increase mortality in mosquitoes (Valkiūnas *et al*., 2014). Thus, bird-mosquito interactions may be driven by arms-races between mosquitoes and parasites, with the latter potentially increasing the attraction of mosquitoes to infected individuals and selection acting on mosquitoes to reduce contact rates with the more virulent parasites that infect birds.

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REFERENCES

Amo, L., Avilés, J.M., Parejo, D., Peña, A., Rodríguez, J. & Tomás, G. (2012). Sex recognition by odour and variation in the uropygial gland secretion in starlings. *Journal of Animal Ecology*, 81: 605-613.

Anderson, R.A., Knols, B.G.J. & Koella, J.C. (2000). *Plasmodium falciparum* sporozoites increase feeding-associated mortality of their mosquito hosts *Anopheles gambiae* s.l. *Parasitology*, 129: 329-333.

Anuradha, V. & Yogananth, N. (2015). Efficacy of mosquito repellent and adulticidal activities of *Halophila ovalis* extract against filaria vectors. *Journal of Tropical Diseases & Public Health,* 4: 2.

Asghar, M., Hasselquist, D., Hansson, B., Zehtindjiev, P., Westerdahl, H. & Bensch, S. (2015). Hidden costs of infection: chronic malaria accelerates telomere degradation and senescence in wild birds. *Science*, 347: 436-438.

Bensch, S., Hellgren, O. & Pérez-Tris, J. (2009). MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Molecular Ecology Resources*, 9: 1353-1358.

Bukauskaitė, D., Bernotienė, R., Iezhova, T.A. & Valkiūnas, G. (2016). Mechanisms of mortality in *Culicoides* biting midges due to *Haemoproteus* infection. *Parasitology*, 143: 1748-1754.

Burguer, B.V., Reiter, B., Borzyk, O. & Du Plessis, M.A. (2004). Avian exocrine secretions. I. chemical characterization of the volatile fraction of the uropygial secretion of the green woodhoopoe, *Phoeniculus purpureus*. *Journal of Chemical Ecology*, 30: 1603-1611.

Burkett-Cadena, N.D., Bingham, A.M. & Unnasch, T.R. (2014). Sex-biased avian host use by arbovirus vectors. *Royal Society Open Science,* 1: 140262.

Choumet, V., Attout, T., Chartier, L., Khun, H., Sautereau, J., Robbe-Vincent, A., Brey, P.,

Downloaded From: https://bioone.org/journals/Ardeola on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Huerre, M. & Bain, O. (2012). Visualizing non infectious and infectious *Anopheles gambiae* blood feedings in naive and saliva-immunized mice. *PLoS One*, 7: e50464.

Christe, P. Møller, A.P. & de Lope, F. (1998). Immunocompetence and nestling survival in the house martin: The tasty chick hypothesis. *Oikos*, 83: 175-179.

Ciloglu, A., Ellis, V.A., Bernotienė, R., Valkiūnas, G. & Bensch, S. (2019). A new one-step multiplex PCR assay for simultaneous detection and identification of avian haemosporidian parasites. *Parasitology Research*, 118: 191-201.

Cornet, S., Nicot, A., Rivero, A. & Gandon, S. (2013a). Malaria infection increases bird attractiveness to uninfected mosquitoes. *Ecology Letters*, 16: 323-329.

Cornet, S., Nicot, A., Rivero, A. & Gandon, S. (2013b). Both infected and uninfected mosquitoes are attracted toward malaria infected birds. *Malaria Journal*, 12: 179.

Cornet, S., Nicot, A., Rivero, A. & Gandon, S. (2019). Avian malaria alters the dynamics of blood feeding in *Culex pipiens* mosquitoes. *Malaria Journal*, 18: 82.

Cozzarolo, C.S., Sironi, N., Glaizot, O., Pigeault, R. & Christe, P. (2019). Sex-biased parasitism in vector-borne disease: Vector preference? *PLoS One,* 14: e0216360.

Dadam, D., Robinson, R.A., Clements, A., Peach, W.J., Bennett, M., Rowcliffe, J.M. & Cunningham, A.A. (2019). Avian malaria-mediated population decline of a widespread iconic bird species. *Royal Society Open Science*, 6: 182197.

Darbro, J.M. & Harrington, L.C. (2007). Avian defensive behavior and blood-feeding success of the West Nile vector mosquito, *Culex pipiens*. *Behavioral Ecology*, 18: 750-757.

De Moraes, C.M., Stanczyk, N.M., Betz, H.S., Pulido, H., Sim, D.G., Read, A.F. & Mescher, M.C. (2014). Malaria-induced changes in host odors enhance mosquito attraction. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 11079-11084.

Díez-Fernández, A., Martínez-de la Puente, J., Gangoso, L., Ferraguti, M., Soriguer, R. & Figuerola, J. (2020a). House sparrow uropygial gland secretions do not attract ornithophilic nor mammophilic mosquitoes. *Medical and Veterinary Entomology*, 34: 225-228.

Díez-Fernández, A., Martínez-de la Puente, J., Gangoso, L., López, P., Soriguer, R., Martín, J. & Figuerola, J. (2020b). Mosquitoes are attracted by the odour of *Plasmodium* infected birds. *International Journal for Parasitology*, 50(8): 569-575.

Garvin, M.C., Austin, A., Boyer, K., Gefke, M., Wright, C., Pryor, Y., Soble, A. & Whelan, R.J. (2018). Attraction of *Culex pipiens* to house sparrows is influenced by host age but not uropygial gland secretions. *Insects*, 9: 127.

Gu, Y.Q., Mo, M.H., Zhou, J.P., Zou, C.S. & Zhang, K.Q. (2007). Evaluation and identification of potential organic nematicidal volatiles from soil bacteria. *Soil Biology and Biochemistry*, 39: 2567-2575.

Gutiérrez-López, R., Martínez-de la Puente, J., Gangoso, L., Yan, J., Soriguer, R. & Figuerola, J. (2019a). Experimental reduction of host *Plasmodium* infection load affects mosquito survival. *Scientific Reports,* 9: 8782.

Gutiérrez-López, R., Martínez-de la Puente, J., Gangoso, L., Soriguer, R. & Figuerola, J. (2019b). Effects of host sex, body mass and infection by avian *Plasmodium* on the biting rate of two mosquito species with different feeding preferences. *Parasites & Vectors*, 12: 87.

Grieves, L.A., Kelly, T.R., Bernards, M.A. & MacDougall-Shackleton, E.A. (2018). Malarial infection alters wax ester composition of preen oil in songbirds: Results of an experimental study. *The Auk*, 135: 767-776.

Heil, M. (2016). Host manipulation by parasites: cases, patterns, and remaining doubts. *Frontiers in Ecology and Evolution*, 4: 80.

Huang, C.B., Alimova, Y., Myers, T.M. & Ebersole, J.L. (2011). Short-and medium-chain fatty acids exhibit antimicrobial activity for oral microorganisms. *Archives of Oral Biology*, 56: 650-654.

Ilgūnas, M., Bukauskaitė, D., Palinauskas, V., Iezhova, T., Fragner, K., Platonova, E., Weissenböck, H. & Valkiūnas, G. (2019a). Patterns of *Plasmodium homocircumflexum* virulence in experimentally infected passerine birds. *Malaria Journal*, 18: 174.

Ilgūnas, M., Palinauskas, V., Platonova, E., Iezhova, T. & Valkiūnas, G. (2019b). The experimental study on susceptibility of common European songbirds to *Plasmodium elongatum*

Downloaded From: https://bioone.org/journals/Ardeola on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(lineage pGRW6), a widespread avian malaria parasite. *Malaria Journal*, 18: 290.

Koella, J.C. (2002). Stage-specific manipulation of a mosquito's host-seeking behavior by the malaria parasite *Plasmodium gallinaceum*. *Behavioral Ecology*, 13: 816-820.

Krause, E.T., Bischof, H.-J., Engel, K., Golüke, S., Maraci, Ö., Mayer, U., Sauer, J. & Caspers, B.A. (2018). Olfaction in the Zebra finch (*Taeniopygia guttata*): what is known and further perspectives. In, M. Naguib, L. Barrett, S.D. Healy, J. Podos, L.W. Simmons & M. Zuk (Eds.): *Advances in the study of behaviour*, pp. 3785. Academic Press.

Lalubin, F., Bize, P., van Rooyen, J., Christe, P. & Glaizot, O. (2012). Potential evidence of parasite avoidance in an avian malarial vector. *Animal Behaviour*, 84: 539-545.

Lehane, M.J. (2005). *The biology of blood-sucking in insects*. Cambridge University Press.

Magallanes, S., Møller, A.P., García-Longoria, L., de Lope, F. & Marzal, A. (2016). Volume and antimicrobial activity of secretions of the uropygial gland are correlated with malaria infection in house sparrows. *Parasites & Vectors*, 9: 232.

Martín-Vivaldi, M., Peña, A., Peralta-Sánchez, J.M., Sánchez, L., Ananou, S., Ruiz-Rodríguez, M. & Soler, J.J. (2009). Antimicrobial chemicals in hoopoe preen secretions are produced by symbiotic bacteria. *Proceedings Biological Sciences*, 277: 123-130.

Martínez, J., Martínez-de la Puente, J., Herrero, J., del Cerro, S., Lobato, E., Rivero-de Aguilar, J., Vásquez, R.A. & Merino, S. (2009). A restriction site to differentiate *Plasmodium* and *Haemoproteus* infections in birds: on the inefficiency of general primers for detection of mixed infections. *Parasitology*, 136: 713-722.

Martínez-de la Puente, J., Merino, S., Tomás, G., Moreno, J., Morales, J., Lobato, E., García-Fraile, S. & Belda, E.J. (2010). The blood parasite *Haemoproteus* reduces survival in a wild bird: a medication experiment. *Biology Letters*, 6: 663-665.

Martínez-de la Puente, J., Rivero-de Aguilar, J., del Cerro, S., Argüello, A. & Merino, S. (2011). Do secretions from the uropygial gland of birds attract biting midges and black flies? *Parasitology Research*, 109: 1715-1718.

Marzal, A., Bensch, S., Reviriego, M., Balbontin, J. & de Lope, F. (2008). Effects of malaria double infection in birds: one plus one is not two. *Journal of Evolutionary Biology*, 21: 979-987.

Merino, S., Potti, J. & Fargallo, J.A. (1997). Blood parasites of passerine birds from central Spain. *Journal of Wildlife Diseases*, 33: 638-641.

Merino, S., Moreno, J., Sanz, J.J. & Arriero, E. (2000). Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). *Proceedings: Biological Sciences*, 267: 2507-2510.

Merino, S., Martínez, J., Martínez-de la Puente, J., Criado-Fornelio, A., Tomás, G., Morales, J., Lobato, E. & García-Fraile, S. (2006). Molecular characterization of the 18S rDNA gene of an avian *Hepatozoon* reveals that it is closely related to *Lankesterella*. *Journal of Parasitology*, 92: 1330-1335.

Niebuhr, C.N., Poulin, R. & Tompkins, D.M. (2016). Is avian malaria playing a role in native bird declines in New Zealand? Testing hypotheses along an elevational gradient. *PLoS One*, 11: e0165918.

Pigeault, R., Vézilier, J., Cornet, S., Zélé, F., Nicot, A., Perret, P., Gandon, S. & Rivero, A. (2015). Avian malaria: a new lease of life for an old experimental model to study the evolutionary ecology of *Plasmodium*. *Philosophical Transactions of the Royal Society of London B*, 370: 20140300.

Reneerkens, J., Versteegh, M.A., Schneider, A.M., Piersma, T. & Burtt, E.H.Jr. (2008). Seasonally changing preen-wax composition: Red Knots' (*Calidris canutus*) flexible defense against feather-degrading bacteria. *The Auk*, 125: 285-290.

Rizzoli, A., Bolzoni, L., Chadwick, E.A., Capelli, G., Montarsi, F., Grisenti, M., Martínez-de la Puente, J., Muñoz, J., Figuerola, J., Soriguer, R., Anfora, G., Di Luca, M. & Rosà, R. (2015). Understanding West Nile virus ecology in Europe: *Culex pipiens* host feeding preference in a hotspot of virus emergence. *Parasites & Vectors*, 8: 213.

Rossignol, P.A., Ribeiro, J.M.C. & Spielman, A. (1986). Increased biting rate and reduced fertility in sporozoite-infected mosquitoes. *The American Journal of Tropical Medicine and Hygiene*, 35: 277-279.

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Rossignol, P.A., Ribeiro, J.M. & Spielman, A. (1984). Increased intradermal probing time in sporozoite-infected mosquitoes. *The American Journal of Tropical Medicine and Hygiene*, 33: 17-20.

Russell, C.B. & Hunter, F.F. (2005). Attraction of *Culex pipiens/restuans* (Diptera: Culicidae) mosquitoes to bird uropygial gland odors at two elevations in the Niagara region of Ontario. *Journal of Medical Entomology*, 42: 301-305.

Santiago-Alarcon, D., Palinauskas, V. & Schaefer, H.M. (2012). Diptera vectors of avian haemosporidian parasites: untangling parasite life cycles and their taxonomy. *Biological Reviews*, 87: 928-964.

Schaber, C.L., Katta, N., Bollinger, L.B., Mwale, M., Mlotha-Mitole, R., Trehan, I., Raman, B. & Odom John, A.R. (2018). Breathprinting reveals malaria-associated biomarkers and mosquito attractants. *The Journal of Infectious Diseases*, 217: 1553-1560.

Shaw, C.L., Rutter, J.E., Austin, A.L., Garvin, M.C. & Whelan, R.J. (2011). Volatile and semi-volatile compounds in Gray Catbird uropygial secretions vary with age and between breeding and wintering grounds. *Journal of Chemical Ecology*, 37: 329-339.

Simpson, J.E. (2009). Avian host-selection by *Culex pipiens* in experimental trials. *PLoS One*, 4: e7861.

Sivakumar, R., Jebanesan, A., Govindarajan, M. & Rajasekar, P. (2011). Larvicidal and repellent activity of tetradecanoic acid against *Aedes aegypti* (Linn.) and *Culex quinquefasciatus* (Say.) (Diptera: Culicidae). *Asian Pacific Journal of Tropical Medicine*, 4: 706-710.

Soini, H.A., Schrock, S.E., Bruce, K.E., Wiesler, D., Ketterson, E.D. & Novotny, M.V. (2007). Seasonal variation in volatile compound profiles of preen gland secretions of the dark-eyed junco (*Junco hyemalis*). *Journal of Chemical Ecology*, 33: 183-198.



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Syed, Z. & Leal, W.S. (2009). Acute olfactory response of *Culex* mosquitoes to a human-and bird-derived attractant. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 18803-18808.

Thiévent, K., Zilio, G., Hauser, G. & Koella, J.C. (2019). Malaria load affects the activity of mosquito salivary apyrase. *Journal of Insect Physiology*, 116: 10-16.

Tomás, G., Merino, S., Martínez-de la Puente, J., Moreno, J., Morales, J. & Lobato, E. (2008). Determinants of abundance and effects of blood-sucking flying insects in the nest of a hole-nesting bird. *Oecologia*, 156: 305-312.

Tuttle, E.M., Sebastian, P.J., Posto, A.L., Soini, H.A., Novotny, M.V. & Gonser, R.A. (2014). Variation in preen oil composition pertaining to season, sex, and genotype in the polymorphic white-throated sparrow. *Journal of Chemical Ecology*, 40: 1025-1038.

Valkiūnas, G. (2005). *Avian malaria parasites and other Haemosporida*. CRC Press, Boca Raton, FL.

Valkiūnas, G., Kazlauskienė, R., Bernotienė, R., Bukauskaitė, D., Palinauskas, V. & Iezhova, T.A. (2014). *Haemoproteus* infections (Haemosporida, Haemoproteidae) kill bird-biting mosquitoes. *Parasitology Research*, 113: 1011-1018.

Van Riper III, C., Van Riper, S.G., Goff, M.L. & Laird, M. (1986). Epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs*, 56: 327-344.

Whittaker, D.J., Rosvall, K.A., Slowinski, S.P., Soini, H.A., Novotny, M.V. & Ketterson, E.D. (2018). Songbird chemical signals reflect uropygial gland androgen sensitivity and predict aggression: implications for the role of the periphery in chemosignaling. *Journal of Comparative Physiology A*, 204: 5-15.

Williams, W.G., Kennedy, G.G., Yamamoto, R.T., Thacker, J.D. & Bordner, J. (1980). 2-Tridecanone: a naturally occurring insecticide from wild tomato *Lycopersicon hirsutum f. glabratum*. *Science*, 207: 888-889.

Yan, J., Gangoso, L., Martínez-de la Puente, J., Soriguer, R. & Figuerola, J. (2017). Avian phenotypic traits related to feeding preferences in two *Culex* mosquitoes. *Naturwissenschaften*, 104: 76.

Yan, J., Martínez-de la Puente, J., Gangoso, L., Gutiérrez-López, R., Soriguer, R. & Figuerola, J. (2018). Avian malaria infection intensity influences mosquito feeding patterns. *International Journal for Parasitology*, 48: 257-264.

Zhang, J.X., Wei, W., Zhang, J.H. & Yang, W.H. (2010). Uropygial gland-secreted alkanols contribute to olfactory sex signals in Budgerigars. *Chemical Senses*, 35: 375-382.

Zhang, Y.H., Du, Y.F. & Zhang, J.X. (2013). Uropygial gland volatiles facilitate species recognition between two sympatric sibling bird species. *Behavioral Ecology*, 24: 1271-1278.

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