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LACK OF BLOOD PARASITES IN BIRD SPECIES: DOES ABSENCE OF BLOOD PARASITE VECTORS EXPLAIN IT ALL?

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SUMMARY.—*Lack of blood parasites in bird species: Does absence of blood parasite vectors explain it all?* The apparent absence of blood parasites in some bird taxa is commonly explained by the absence or scarcity of parasite vectors in some habitats such as marine, saline, arid, open, alpine or high latitude environments. However, in addition to such extrinsic factors, immunological capabilities of the host and absence of the right host-parasite assemblage might also be important. In this paper, we suggest that extant hypotheses are not mutually exclusive and may act simultaneously at different hierarchical levels. Hence, one should consider all explanations equally to prevent inadequate generalizations. Additionally, we suggest a new hypothesis, according to which highly mobile ectoparasites might exclude the dipteran vectors of blood parasites in bird species with high prevalences and intensities of ectoparasites.

Key Words: blood parasites, immunocompetence, review, host-parasite specificity, vectors.

RESUMEN.—*¿Explica la ausencia de vectores la falta de parásitos sanguíneos en ciertas especies de aves?* Este trabajo discute si la aparente ausencia de parásitos sanguíneos en diversos grupos de aves se puede deber únicamente a la escasez o ausencia de dípteros vectores de hemoparásitos en medios salinos, marinos, áridos, abiertos, alpinos o de latitudes altas. A pesar de que ésta es la explicación más común en la bibliografía existente, se pueden encontrar contradicciones en la propia bibliografía que demuestran que la ausencia de vectores no es una explicación universal. En primer lugar, es importante asegurarse de que no están operando factores que puedan sesgar la detectabilidad de los parásitos (v.g. empleo de métodos inadecuados de detección) o afectar a la susceptibilidad de parasitación de los hospedadores (v.g. variaciones respecto a edad, sexo, conducta o hábitat). Asimismo, hay que tener en cuenta explicaciones alternativas tales como la ausencia del parásito adecuado (v.g. fisiológica y ecológicamente compatible) para un hospedador dado a pesar de la presencia de vectores en el medio y parásitos en especies sintópicas, debido a la gran especificidad hospedador/huésped a nivel de familia taxonómica. Un factor más a tener en cuenta es la fortaleza del sistema inmune del hospedador, que puede variar grandemente entre grupos de aves en función de sus rasgos de vida (por ejemplo, tasas de crecimiento, esfuerzo reproductor). Las tres hipótesis básicas han de tenerse en cuenta a la vez ya que no son mutuamente excluyentes y actúan a niveles jerárquicos distintos. Esto implica que hay que evitar la generalización de explicaciones válidas para una especie a especies que habiten en am-

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bientes análogos. Finalmente, se propone una nueva hipótesis, únicamente como ejercicio para mostrar la complejidad del tema abordado, según la cual la ausencia de hemoparásitos en grupos de aves con altas cargas de ectoparásitos móviles (por ejemplo, aves marinas) podría deberse a cierta exclusión competitiva de los vectores de los parásitos sanguíneos por parte de los ectoparásitos.

Palabras clave: parásitos sanguíneos, inmunocompetencia, revisión, especificidad parasito-hospedador, vectores.

Many studies have addressed the prevalence of blood parasites in bird populations (see checklists by Greiner *et al.*, 1975; Peirce, 1981), with more than 4,000 species examined and more than 2,500 found to be infected at least with one species of blood parasite. Species found to be apparently free of blood parasites include some raptors (Blanco *et al.*, 1998; Martínez-Abraín & Urios, 2002), seabirds (González-Solís & Abella, 1997; Merino & Mínguez, 1998; Engstrom *et al.*, 2001; Jovani *et al.*, 2001), passerines and Phasianinae inhabiting islands (Little & Earlé, 1994; Stewart *et al.*, 1997), South African Sandgrouse and weavers (Little & Earlé, 1995), storks (Jovani *et al.*, 2002), swifts (Tella *et al.* 1995), waders (Figueroa *et al.*, 1996), nightjars (Forero *et al.*, 1997), and high-latitude passerines (Rytönen *et al.*, 1996).

Absence of blood parasites has been commonly attributed to the absence or scarcity of appropriate vectors (Bennett *et al.*, 1992a, 1992b, 1995; Little & Earlé, 1995; Tella *et al.*, 1996; Piersma, 1997; Figuerola, 1999; Sol *et al.*, 2000; Jovani *et al.*, 2001; Martínez-Abraín & Urios, 2002; Valera *et al.*, 2003) despite scarce ecological knowledge of these. Lack of blood parasites has also been attributed to the good immunological capabilities of the host (Ricklefs, 1992; Forero *et al.*, 1997; Merino & Mínguez, 1998; Tella *et al.*, 1999) and to lack of a suitable (i.e. referring mainly to physiological compatibility) host-parasite assemblage (Earlé & Underhill, 1993; Little & Earlé, 1994; Stewart *et al.*, 1997; Blanco *et al.*, 1998; Jones & Shellam, 1999). Some apparently alternative explanations, such as low host density or insufficient time for the co-evolution of host, vectors and parasite to have occurred (see Bennett, 1992; Earlé & Underhill, 1993; Rytönen *et al.*, 1996; González-Solís & Abella, 1997; Valera *et al.*, 2003), are included within the latter hypothesis (i.e. lack of a suitable host-parasite assemblage).

Many species with negative records of blood parasites inhabit vector-poor habitats (e.g.

salty or marine environments, high altitude or latitude zones, windy, arid or open areas), but scarcity of suitable ornithophilic vectors cannot explain the pattern completely. In fact a number of contradictions can be readily identified reviewing the information published so far:

(1) One finds cases of pairs of syntopically breeding species in which one is infected and a second species is apparently free of haematozoa. Some *Diomedea* albatross species from sub-Antarctic South Georgia were infected with *Hepatozoon albatrossi*, whilst petrels and prions were not (Peirce & Prince, 1980). At the Chafarinas Islands, Cory's Shearwaters *Calonectris diomedea* had no blood parasites whereas Audouin's Gull *Larus audouinii* and Yellow-legged Gull *L. cachinnans* (even pre-fledging chicks) were infected (see Ruiz *et al.*, 1995; González-Solís & Abella, 1997).

(2) Cases occur in which species linked to saline habitats exhibited higher prevalences than closely related species typical of freshwater habitats (see Table 1 in Figuerola, 1999).

(3) Absence of blood parasites in White Storks *Ciconia ciconia* (Jovani *et al.* 2002) is also striking, considering that these species forage in freshwater habitats where vectors are typically abundant. For instance, 76% of the freshwater ducks from Labrador and insular Newfoundland ($n = 510$) examined by Bennett *et al.* (1991) were parasitized by one or more haematozoa.

(4) Forero *et al.* (1997) found no blood parasites in Red-necked Nightjars *Caprimulgus ruficollis* captured at Doñana National Park, a region of marshes and Mediterranean forests where vectors are probably abundant.

Hypotheses formulated so far are not mutually exclusive, and all of them could be acting at the same time (absence of vectors, absence of the right host-parasite assemblage, high host immunocompetence) but at different hierarchical levels (see Table 1).

TABLE 1

Main hypothesis developed to explain the lack of blood parasites in certain bird groups. A new hypothesis suggested in the present study has been included.

[Principales hipótesis desarrolladas para explicar la falta de parásitos sanguíneos en ciertos grupos de aves. Una nueva hipótesis sugerida en el presente estudio ha sido incluida.]

Hypothesis [Hipótesis]	Scale of application [Escala de aplicación]	Year of first statement [Año de aparición]	References [Referencias]
Absence of vectors	Ecological	1992	Bennett <i>et al.</i> (1992a, 1992b)
Host-parasite assemblage	Evolutionary	1993	Bennett <i>et al.</i> (1993, 1994)
Host immunological capabilities	Ecophysiological	1992	Ricklefs (1992)
Competitive exclusion by ectoparasites	Ecological	2004	The present study

ABSENCE OF PARASITES: VARIATIONS IN THE SUSCEPTIBILITY OF THE HOST OR LOW PARASITE DETECTABILITY?

Apparent absence of blood parasites can be an artefact caused by low parasite detectability or by intraspecific variation in the susceptibility of the host to parasitisation depending on age, sex, behaviour or habitat:

(1) Rytkönen *et al.* (1996) found that Willow Tits *Parus montanus* from Finnish coniferous forests were free of blood parasites, whereas other resident *Parus* species were infected. However, Rintamäki *et al.* (2000) found a prevalence of 14.5% for the same tit population sampled later in the season, when nestlings had already fledged, showing that the absence of blood parasites in this species was an artefact due to sampling date (i.e. age of nestlings).

(2) Blanco *et al.* (1998) found no blood parasites in Griffon Vultures *Gyps fulvus* in Spain whereas Merino *et al.* (2002) found them infected with *Babesia moshkovskii*. Differences could be attributed in part to a different origin of birds but also to the difficult detection of the small *Babesia* spp. parasites.

(3) Differences in host habitat (e.g. temperature) can affect feeding activity of dipteran vectors (see Allander & Bennett, 1994).

(4) Serological studies have suggested that exposure to *Plasmodium* spp. in wild penguins may be more widespread than can be detected by direct blood examination, especially in temperate species (see Jones & Shellam, 1999).

(5) Techniques used for the detection of blood parasites have differential success de-

pending upon parasite species. For instance, cyto centrifugation has shown better results than thick films in the recovery of microfilariae and *Plasmodium* spp. in mammalian cells (Petithory *et al.*, 1997). However, the utility of this technique remains to be tested in birds with nucleated red blood cells. Quantitative buffy coat (QBC) and polymerase chain reaction (PCR) are also most appropriate for low parasitaemias (Bensch *et al.*, 2000; Ricklefs & Fallon, 2001). Also, centrifugation of haematocrit tubes is the most reliable method for the detection of low parasitaemias and the determination of the number of trypanosomes in a given volume of blood (Bennett, 1962; Woo, 1969). Cooper & Anwar (2001) stated that *Plasmodium* in penguins should be best explored in impression smears of lung, spleen or liver because they can be present but not readily detected in blood, which would probably be true of any malarial parasite.

Hence, much care has to be taken when reporting absence of blood parasites to account for intraspecific variation in susceptibility to haemoparasites (see Allander & Bennett, 1994; Møller *et al.*, 1998) as well as detectability of parasites.

HOST-PARASITE ASSEMBLAGES

Working with ectoparasites, Fain (1977) found some specialization of species of mites with respect to their mammalian hosts. Moreover, Hafner & Nadler (1988) showed that phylogenetic trees of rodents and their ecto-

parasites were topologically concordant, both in branching pattern and branch length, suggesting coevolution of hosts and parasites. Similarly, Tella *et al.* (1998) found high host specificity in bird species parasitized by a louse fly.

This rule seems to hold as well for blood parasites and their hosts. Atkinson (1986) found some host specificity among farm birds infected experimentally with *Haemoproteus*. Morphological work by Bennett *et al.* (1993, 1994) suggested that blood parasite species are restricted to host taxonomic families. More recently molecular studies by Bensch *et al.* (2000) and Ricklefs & Fallon (2001) confirmed this suggestion by showing highly significant host fidelity among bird malaria blood parasites (both *Plasmodium* and *Haemoproteus*), with host switching being infrequent, and again suggesting significant association between hosts and parasites. This specificity suggests that although a given blood parasite is detected in a bird community, host species not closely-related can be free of blood parasites despite the presence of appropriate vectors in the area. As a corollary, such specificity suggests that a given bird species should be less likely to be infected by a blood parasite in small communities (such as island communities), where the probability of living with an closely related species that harbours a parasite population is lower than in larger, more diverse, mainland bird communities.

THE ROLE OF IMMUNOCOMPETENCE

Ricklefs (1992) found that in non-raptorial, altricial land birds prevalence of blood parasites was inversely related to the length of the incubation period. This relationship could be caused by a link between duration of the embryonic development and ability to resist or control infection, owing to maturational processes in the avian immune system. In this context, Tella *et al.* (1999) confirmed that prevalence is inversely correlated to the embryonic development period even among closely related birds, supporting the possible link between immune performance and prevalence of haemoparasites. We have recently shown elsewhere (Esparza, *et al.*, 2004) that European Storm-petrels *Hydrobates pelagicus* from the

colony located on the island of Benidorm (SE Spain) have a much stronger response to the PHA assay (a test that measures a T-lymphocyte-dependent component of immunocompetence) than syntopically breeding Yellow-legged Gulls *Larus michahellis*. Storm-petrels are apparently free of blood parasites on that island (Merino & Mínguez, 1998; *pers. obs.*), although highly infested with fleas, mites, soft ticks and lice (Merino *et al.*, 1999). In contrast, pre-fledging Yellow-legged Gull chicks were found to be infected with *Babesia bennetti* (Merino, 1998; Esparza, *et al.*, 2004) whose vector is probably a tick, and adults become highly infected by *Haemoproteus lari*, which they probably acquire on garbage dumps located a few kilometres away on the mainland coast since *Culicoides* vectors have not been captured on the island (Martínez-Abraín *et al.*, 2002). Yellow-legged Gulls from Benidorm are also commonly infected with diarrhoea-causing bacteria (*pers. obs.*). Bosch & Muniesa (1996) described a similar case at the Medas Islands (NE Spain).

Our data suggests a possible role of immunocompetence in preventing infection by blood parasites in Storm-petrels, which might apply to other oceanic seabirds. Despite of the presence of appropriate vectors and the right host-parasite assemblage in the environment, birds could be free of blood parasites if the competence of their immune system is extremely high, owing either to the direct evolution of the immune system to fight against pathogens other than blood parasites (e.g. bacteria, viruses) or as a by-product of the evolution of a strong immune system and good repair mechanisms for a long life span. Storm-petrels, for instance, weigh only 28 g but may live up to 40 years, which is the average life span of a chimpanzee, suggesting that their physiology and immunology could be very special. However, we cannot exclude the influence of factors other than immunocompetence (e.g. problems faced by parasites to complete their life cycles in bird species that spend a large part of the year at sea, or absence of physiological compatibility between *Babesia* and storm-petrels) on this pattern of absence of blood parasites in Storm-petrels.

MARINE SHOREBIRDS VERSUS SEABIRDS:
A CALL FOR MORE TAXON-SPECIFIC
EXPLANATIONS

Findings for one taxonomic group need not be appropriate for another group living in analogous ecological conditions. Piersma (1997) suggested that waders breeding in the arctic tundra and wintering along temperate seashores, as well as seabirds, are typically free of blood parasites because they make use of habitats where parasite vectors are scarce or absent. We agree that his hypothesis has a great explanatory power but we would not include seabirds within the same box. As argued before (see: the role of immunocompetence), seabirds live in marine environments where parasite vectors are not common but might *in toto* or in part be free of blood parasites because of mechanisms related to their slow embryonic development and their long life span. That does not contradict Piersma's (*op. cit.*) statement that marine shorebirds are long-lived compared to non-marine Charadriiformes because they live in parasite-poor environments. All we argue is that patterns found for one group cannot or should not be generalized to other distant taxonomic groups because of ecological affinities. This may lead to a mistake similar to the confounding of homology and common descent when classifying species.

AN ALTERNATIVE HYPOTHESIS: COMPETITIVE
EXCLUSION OF HAEMOPARASITE VECTORS
MEDIATED BY ECTOPARASITES

In addition to the three main explanations for the absence of blood parasites in some species, alternative explanations can be suggested simply as an exercise to show the complexity of the topic.

Many bird species that have been found to be free of haemoparasites are highly infested with ectoparasites. We suggest that some sort of biological interaction might occur between some ectoparasite groups (e.g. highly mobile species such as wingless flies and fleas whose role as blood parasite vectors is unclear) and dipteran blood parasite vectors. Accordingly, bird species with high prevalences and intensities of these mobile ectoparasites could obtain physical defence against biting flies and mos-

quitoes that transmit blood parasites (e.g. ectoparasites could attack biting dipterans or modify host physiological cues to make them less attractive to dipteran vectors). From an evolutionary perspective, ectoparasites would defend their hosts from further and more virulent exploitation, similar to the well-known mutualistic case of ants that defend the acacia plants that provide them with food and nesting sites (Janzen, 1966). This could well be the case for long-lived Procellariiformes (storm-petrels, shearwaters) and alpine swifts, which are highly infested with ectoparasites but apparently free of haemoparasites (González-Solís & Abella, 1997; Merino & Mínguez, 1998; Tella *et al.*, 1998). Although ectoparasites can have a cost for hosts (see, for example, Merino *et al.*, 1999), they do not cause host death in the manner of some blood parasites, such as *Plasmodium*. Hence, under some circumstances, ectoparasites could have an overall positive effect for hosts. Competitive exclusion of blood parasite vectors in some bird species could be mediated by their own ectoparasites. If this were true, the artificial removal of all ectoparasites from a bird could lead to its destruction. It could also happen that the immune response mounted against the effect of ectoparasites could protect hosts from microparasite infections, as seemingly happens between some blood parasite species (Cox, 2001).

SUMMARIZING: NON-MUTUALLY EXCLUSIVE
HYPOTHESES ACCOUNT FOR BIOLOGICAL
COMPLEXITY

We do not reject the absence or scarcity of vectors as a possible explanation for the apparent absence of blood parasites in some bird groups. However, we think that experimental approaches should be employed whenever possible to show the role of absence of vectors (see for example, Sol *et al.*, 2000). In addition, alternative explanations to absence of suitable parasite vectors should be explored further for each taxonomic group, even though lack of vectors seems an appropriate explanation. We should avoid generalizations and make sure that although blood parasite vectors are absent in a given study area, we find negative evidence for alternative hypothesis. For instance, the absence of blood parasites in a bird species in-

habiting an arid zone should be tested at least by (a) attempting to trap proper vectors, (b) measuring the immunological capabilities of the host, and (c) sampling closely related species for blood parasites to check the presence/absence of the right parasite in the area. One could argue that if appropriate vectors are absent there is no point in pursuing alternative hypotheses, such as high immune competence or absence of suitable parasites. However, these matters are important at least from a conservation perspective. The introduction of a vector in a given community means nothing unless the right parasite is also present and the immune system of the host is not able to prevent infection (see for example, Van Riper III *et al.*, 1986; Warner, 1968). Life is diverse and so should our explanations.

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