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BLOOD PARASITES OF SOME BIRDS FROM KENYA, TANZANIA AND ZAIRE

GORDON F. BENNETT and CARLTON M. HERMAN¹

Abstract: A total of 647 birds of 146 species representing 41 families from localities in Kenya, Tanzania and Zaire were examined for blood parasites. A total of 242 (37.2%) birds harbored either single or multiple infections of *Haemoproteus* (16%), *Leucocytozoon* (14%), *Plasmodium* (5.4%), *Trypanosoma* (1.7%), microfilaria (2.9%) or a variety of babesioids and haemogregarines (4.3%). Occurrence of blood parasites was greatest in Zaire and least in Kenya; the occurrence of the different genera varied markedly between areas and between bird families.

INTRODUCTION

In the early part of the century, the blood parasites of African birds received considerable attention and many species of hematozoa were described from them. In recent years, relatively few studies on the hematozoa of African birds have been published. Such published accounts that are available, with the notable exceptions of those of Tendeiro³ and Travassos Santos Dias,⁴ usually diagnose the parasites to the generic level only and rarely present data indicating prevalence or distribution. As a result, little is known concerning the abundance and species distribution of the blood parasites of the African avifauna.

During the past years, the International Reference Center for Avian Malarial Parasites has acquired, through various sources, collections of blood films from various avian populations in Africa. The results of the examinations from three such collections from Kenya, Tanzania and Zaire are presented here to provide some baseline information on the prevalence, species composition and species distribution of the blood parasite fauna of some birds, primarily passeriforms, of these three areas.

MATERIALS AND METHODS

Blood films were obtained by a variety of means from birds in various localities in Kenya, Tanzania and Zaire. The smears were air-dried, fixed in 100% ethanol or methanol and stained with Giemsa's stain. A minimum of 20,000 erythrocytes were examined on each side.

Birds from Kenya were collected (CMH) in March, 1939, in the vicinity of Kabete, Langata Forest or Lake Naivasha, usually by shooting. All birds were identified by Dr. V. G. L. Van Someren, then Curator, Coryndon Museum, Nairobi. *Plasmodium durae* Herman 1939 was described from the material from turkeys cited in this survey.

Birds from Tanzania were collected by Drs. G. White and W. J. Crans in 1970-71, in the environs of Amani. The birds were usually captured in nets and the population was sampled over a 12-month period.

Birds from Zaire were obtained by M. Lips in 1952, primarily in November-December, in the environs of Lumumbashi (Elizabethville). This collection was presented to the International Reference Center after passing through an unknown number of hands. The smears, apparently made from dead birds, appear to be

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stained with Giemsa's. *Haemoproteus telfordi* Bennett, Forrester, Greiner and Campbell 1975 was described from an otid, *Lisotis melanogaster*, from this collection.

RESULTS AND DISCUSSION

Blood films from 647 birds of 146 species representing 41 families (Table 1) were examined for hematozoans. A total of 242 (37%) birds harbored one or more parasites (Tables 1, 2). The most frequently encountered parasite genus was *Haemoproteus* (16%), represen-

ted by 13 species considered to be valid, and a number of infections which are not as yet diagnosed as to species as the haemoproteids of such families (e.g.—Falconidae, Meropidae) need taxonomic clarification. The genus *Leucocytozoon* was nearly as common as *Haemoproteus* and was represented by 10 species (Table 1). The remaining groups of blood parasites occurred much less frequently (Table 2), with *Plasmodium* represented by only four species. The few infections with trypanosomes and microfilaria can probably be ascribed, in large part, to the inadequacy of the method of diagnosis.^{1,2}

TABLE 1. Hematozoa in birds from Kenya, Tanzania and Zaire. Data is expressed as total number examined/number infected.

ALAUDIDAE. *Mirafra africanoides*: Kenya — 3/0. Total: 3/0.

ALCEDINIDAE. *Halcyon albiventris*: Tanzania — 8/1; babesiod. Total: 8/1.

ANATIDAE. *Alapochen aegypticus*: Kenya — 4/0. *Anas clypeata*: Kenya — 1/0. *Anas crecca*: Kenya — 1/0. *Anas erythrorhynchus*: Kenya — 3/0. *Anas platyrhynchos* (domestic): Tanzania — 43/16; 16 babesiods (*Aegyptianella*), one unidentified *Plasmodium*. *Anas punctata*: Kenya — 8/0. *Anas querquedula*: Kenya — 1/0. *Anas undulata*: Kenya — 5/0. *Anser anser*: Tanzania — 6/0. *Oleotropterus gambensis*: Kenya — 1/0. Total: 78/16.

CAMPEPHAGIDAE. *Coracina caesis*: Kenya — 2/0. Total: 2/0.

CAPITONIDAE. *Buccanodon leucotis*: Tanzania — 16/3; two unidentified leucocytozoids, one *Plasmodium vaughani*. *Buccanodon olivacea*: Tanzania — 8/0. *Pagoniulus bilineatus*: Kenya — 1/0. *Stactolaenia whytii*: Zaire — 1/0. *Trachyphonus erythrocephalus*: Kenya — 1/1; unidentified *Haemoproteus*. *Tricholaema diadematum*: Kenya — 1/0. Total: 28/4.

CAPRIMULGIDAE. *Caprimulgus europaeus*: Tanzania — 1/0. Total: 1/0.

CHARADRIIDAE. *Atephanileyx coronatus*: Kenya — 1/0. *Hoploterus armatus*: Kenya — 3/0. Total: 4/0.

COLIIDAE. *Colius striatus*: Kenya — 11/0; Tanzania — 3/0. Total: 14/0.

COLUMBIDAE. *Columba guinea*: Kenya — 1/1; *Haemoproteus columbae*. *Streptopelia lugens*: Kenya — 2/1; *Leucocytozoon marchouxi*. *Streptopelia semitorquata*: Kenya — 4/4; four with *Haemoproteus columbae*, one with *Leucocytozoon marchouxi*. *Streptopelia senegalensis*: Kenya — 1/1; microfilaria. *Streptopelia* sp.: Zaire — 1/0. *Treron calva*: Kenya — 1/0. *Turtur chalcospilos*: Kenya — 1/0. *Turturoena delegorguei*: Tanzania — 1/0. *Tympanistra tympanistra*: Tanzania — 4/3; two with *Haemoproteus columbae*, two with *Leucocytozoon marchouxi*. Total: 16/10.

TABLE 1 (Continued)

- CORACIIDAE. *Coracias caudata*: Kenya — 1/1; *Haemoproteus coraciae*, *Leucocytozoon* sp. *Coracias spatulata*: Zaire — 2/1; *Haemoproteus coracias*, *Leucocytozoon eurytomi*. *Eurystomus glaucurus*: Zaire — 2/1; *Haemoproteus coraciae*. Total: 5/3.
- CUCULIDAE. *Centropus superciliosus*: Tanzania — 1/0. *Cuculus canorus*: Tanzania — 1/0. Total: 2/0.
- DICRURIDAE. *Dicrurus adsimilis*: Tanzania — 10/2; one babesoid, one with *Leucocytozoon* sp. Total: 10/2.
- EMBERIZIDAE. *Emberiza cabanisi*: Tanzania — 2/2; two with *Leucocytozoon fringillinarum*, one with *Haemoproteus fringillae*. Total: 2/2.
- ESTRILIDAE. *Estrilda astrild*: Tanzania — 1/0. *Estrilda paludicola*: Zaire — 2/1; one with *Haemoproteus fringillae*. *Lagonosticta senegala*: Kenya — 3/0; Zaire — 1/1; *Leucocytozoon fringillinarum*. *Lonchura cucullata*: Zaire — 4/2; two with *Haemoproteus fringillae*; Tanzania — 5/1; one with *Haemoproteus fringillae*. *Pytelia afra*: Zaire — 1/1; microfilaria. *Urogenthus bengalus*: Kenya — 2/0. Total: 19/6.
- FALCONIDAE. *Accipiter tachiro*: Tanzania — 1/1; *Leucocytozoon toddi*, unidentified *Haemoproteus*. *Aquila* sp.: Zaire — 1/1; unidentified *Haemoproteus*. *Circus aeruginosus*: Kenya — 1/0. *Melierax gabar*: Zaire — 2/0. Total: 5/2.
- FRINGILLIDAE. *Carduelis citrinelloides*: Tanzania — 2/1; *Leucocytozoon fringillinarum*. *Serinus atrochularis*: Kenya — 1/1; *Leucocytozoon fringillinarum/majoris*. *Serinus mozambicus*: Zaire — 1/1; *Leucocytozoon fringillinarum/majoris*. Total: 4/3.
- HIRUNDINIDAE. *Hirundo senegalensis*: Tanzania — 2/0. *Psalidoprocne holome-laena*: Tanzania — 7/10. *Ptonoprogne fuligula*: Tanzania — 2/1; unidentified *Haemoproteus*. Total: 11/1.
- LANIIDAE. *Dryoscopus cubla*: Zaire — 1/1; *Haemoproteus lanii*, microfilaria. *Lanius collaris*: Kenya — 30/15; 13 *Haemoproteus lanii*, one *Leucocytozoon fringillinarum/majoris*, one *Plasmodium relictum*. Zaire — 1/1; *Leucocytozoon fringillinarum/majoris*. *Lanius collurio*: Tanzania — 4/3; three with *Haemoproteus lanii*, one *Plasmodium vauhani*. Zaire — 1/0. *Laniarius ferrugineus*: Kenya — 1/1; *Leucocytozoon fringillinarum/majoris*. *Tchagara minuta*: Zaire — 1/1; *Haemoproteus lanii*. *Tchagara senegala*: Kenya — 1/0. Total: 43/22.
- LARIIDAE. *Larus cirricephalus*: Kenya — 2/0. *Hydroprogne tschegrava*: Kenya — 1/0. Total: 3/0.
- MELEAGRIDIDAE. *Meleagris gallopavo*: Kenya — 74/1; *Plasmodium durae*, type host and individual. Total: 74/1.
- MEROPIDAE. *Mellitophagus bullockoides*: Kenya — 5/0. Total: 5/0.
- MOTACILLIDAE. *Anthus novaeseelandias*: Kenya — 4/0. *Motacilla flava*: Kenya — 2/0. Total: 6/0.

TABLE 1 (Continued)

- MUSICAPIDAE.** *Batis malitor*: Kenya — 1/0. *Bradornis pumilus*: Tanzania — 3/2; one *Leucocytozoon fringillinarum* and *Plasmodium vaughani*, one *Haemoproteus* sp. *Dioptrornis fischeri*: Kenya — 1/1; either *Plasmodium* or *Haemoproteus*, too immature to determine. *Parisoma lugens*: Kenya — 1/0. *Tchitreia nigriceps*: Tanzania — 1/1; *Nuttalia* sp. *Tchitreia viridis*: Kenya — 3/0. Total: 10/4.
- MUSOPHAGIDAE.** *Musophago violacea*: Zaire — 2/1; *Leucocytozoon fringillinarum* and *Plasmodium vaughani*. *Tauraco hartlaubi*: Kenya — 1/1; *Haemoproteus montezi*. *Tauraco livingstonii*: Zaire — 2/2; one *Haemoproteus montezi*, one haemogregarine. Total: 5/4.
- NECTARINIIDAE.** *Anthropetes collaris*: Kenya — 1/1; *Leucocytozoon* sp., few, distorted and not identifiable. Tanzania — 6/5; three *Leucocytozoon fringillinarum*, three *Haemoproteus* sp., one *Plasmodium vaughani*, one *Trypanosoma avium*, one *Nuttalia* sp. *Cyanomitra olivacea*: Tanzania — 55/42; three *Leucocytozoon fringillinarum*, 28 *Haemoproteus montezi*, 8 *Plasmodium vaughani*, two *Plasmodium rouxi*, one *Plasmodium relictum*, one *Trypanosoma avium*, six microfilaria, three *Nuttalia* sp. *Nectarina amethystina*: Zaire — 3/2; one *Leucocytozoon fringillinarum*, two *Haemoproteus montezi*, two microfilaria. *Nectarinia kilimensis*: Kenya — 7/1; *Leucocytozoon fringillinarum/majoris* and microfilaria. *Nectarinia senegalensis*: Kenya — 1/1; *Haemoproteus* sp., rare. *Nectarinia venust*: Kenya — 1/1, *Haemoproteus* sp. and *Leucocytozoon* sp., rare. Total: 74/53.
- NUMIDIDAE.** *Guttera pucherani*: Tanzania — 1/1, *Leucocytozoon neavei*, *Plasmodium relictum*. *Numidia meleagris*: Kenya — 1/1, *Leucocytozoon neavei*; Tanzania — 6/3, one *Leucocytozoon neavei*, two *Trypanosoma avium*; Zaire — 5/5, four *Leucocytozoon neavei*, three *Haemoproteus pratezi*, two microfilaria. Total: 13/9.
- ORIOLOIDAE.** *Oriolus auratus*: Zaire — 1/1, *Leucocytozoon fringillinarum*, *Trypanosoma avium*, microfilaria. Total: 1/1.
- OTIDAE.** *Lissotis melanogaster*: Zaire — 2/2, *Haemoproteus telfordi*, type and paratype individuals.
- PHALACROCORACIDAE.** *Haliastur africanus*: Kenya — 2/0. *Phalacrocorax carbo*: Kenya — 1/0. Total: 3/0.
- PHASIANIDAE.** *Francolinus* sp.: Zaire — 1/1, *Leucocytozoon sabrazi*, *Pternistes leucoscepus*: Kenya — 1/0. *Gallus gallus*: Tanzania — 6/1, *Leucocytozoon sabrazi*. Total: 8/2.
- PICIDAE.** *Dendrocopos fuscescens*: Tanzania — 1/0. *Jynx rufficollis*: Kenya — 1/0. *Meopicos goertae*: Kenya — 1/0. Total: 3/0.
- PLOCEIDAE.** *Amaurestes fringiloides*: Tanzania — 6/2, two *Nuttalia* sp. *Amylospiza albifrons*: Kenya — 1/0; Tanzania — 1/0. *Coliuspasser hartlaubi*: Zaire — 3/2, two *Plasmodium vaughani*. *Euplectes ardens*: Zaire — 3/3, *Haemoproteus fringillae*. *Hyphanturgis ocularis*: Tanzania — 6/3, two *Leucocytozoon fringillinarum*, one *Haemoproteus fringillae/orizivora*, one *Plasmodium rouxi*, one *Trypanosoma avium*. *Mandingoa nitidula*: Tanzania — 11/2, one *Leucocytozoon fringillinarum*, one *Haemoproteus fringillae*. *Othypantes stuhlmanni*: Tanzania — 1/1, *Leucocytozoon fringillinarum*, one *Haemoproteus fringillae*, one

TABLE 1 (Continued)

<p><i>Plasmodium vauhani</i>. <i>Passer iagoensis</i>: Kenya — 1/1, <i>Leucocytozoon fringillinarum</i>. <i>Ploceus baglafecht</i>: Kenya — 3/2, two <i>Leucocytozoon fringillinarum</i>; Tanzania — 12/10, one <i>Nuttalia</i> sp., three <i>Leucocytozoon fringillinarum</i>, seven <i>Haemoproteus orizivora</i>. <i>Ploceus ocularia</i>: Kenya — 1/1, <i>Leucocytozoon fringillinarum</i>. <i>Ploceus reichenowi</i>: Kenya — 1/1, <i>Leucocytozoon fringillinarum</i>, <i>Haemoproteus fringillae</i>. <i>Ploceus spekei</i>: Kenya — 9/2, two <i>Leucocytozoon fringillinarum</i>. <i>Ploceus xanthops</i>: Zaire — 1/0. <i>Quelea erythropis</i>: Tanzania — 1/1, <i>Plasmodium rouxi</i>. <i>Quelea quelea</i>: Zaire — 2/2, two <i>Haemoproteus fringillae/orizivora</i>. Total: 72/34.</p>
<p>PYCNONOTIDAE. <i>Andropadus importunus</i>: Tanzania — 7/2, one <i>Nuttalia</i> sp., one <i>Leucocytozoon brimonti</i>. <i>Phyllastrephus fischeri</i>: Kenya — 1/1, <i>Haemoproteus</i> sp. <i>Pyconotus barbatus</i>: Kenya — 4/2, one <i>Haemoproteus</i> sp., one <i>Plasmodium rouxi</i>; Zaire — 8/6, six <i>Leucocytozoon brimonti</i>, one <i>Haemoproteus</i> sp. <i>Pyconotus gracilirostris</i>: Kenya — 1/0. <i>Pyconotus xanthopygus</i>: Tanzania — 31/30, one <i>Nuttalia</i> sp., 29 <i>Leucocytozoon brimonti</i>, two <i>Haemoproteus</i> sp., two <i>Plasmodium rouxi</i>, one <i>Trypanosoma avium</i>, one <i>Lankesterella</i> sp., three microfilaria. Total: 52/41.</p>
<p>RALLIDAE. <i>Fulica cristata</i>: Kenya — 10/0. <i>Limnocorax flavirostro</i>: Kenya — 1/0. <i>Porphyrio madagascariensis</i>: Kenya — 1/0. Total: 12/0.</p>
<p>SCOLOPACIDAE. <i>Capella gallinago</i>: Kenya — 2/0. <i>Capella nigropennis</i>: Kenya — 1/0. <i>Erolia temminckii</i>: Kenya — 1/0. <i>Tringa glariola</i>: Kenya — 1/0. Total: 5/0.</p>
<p>STRIGIDAE. <i>Bubo africanus</i>: Zaire — 1/1, <i>Leucocytozoon ziemanni</i>, <i>Haemoproteus noctuae</i>. <i>Bubo vosseleri</i>: Tanzania — 2/1, <i>Haemoproteus syrnii</i>. Total: 3/2.</p>
<p>STURNIDAE. <i>Cinnyricinclus leucogaster</i>: Zaire — 1/1, <i>Haemoproteus sturnii</i>. <i>Lamprocolius corruscus</i>: Tanzania — 3/1, <i>Leucocytozoon fringillinarum/majoris</i>. <i>Lamprotornis chalybaeus</i>: Kenya — 4/2, one <i>Leucocytozoon fringillinarum/majoris</i>, one <i>Plasmodium relictum</i>; Zaire — 2/1, <i>Haemoproteus sturnii</i>. <i>Lamprotornis chloropterus</i>: Zaire — 1/1, <i>Haemoproteus sturnii</i>. <i>Spreo superbus</i>: Kenya 1/0. <i>Unichognathus walleri</i>: Tanzania — 1/1, <i>Haemoproteus sturnii</i>. Total: 13/7.</p>
<p>SYLVIIDAE. <i>Calamocichla gracilirostris</i>: Kenya — 2/0. <i>Cisticola chiniana</i>: Kenya — 1/0. <i>Cisticola erythropis</i>: Tanzania — 3/0. <i>Cisticola robusta</i>: Kenya — 5/2, one <i>Leucocytozoon fringillinarum</i>, two microfilaria. <i>Phylloscapys trochilus</i>: Kenya — 1/1, <i>Haemoproteus</i> or <i>Plasmodium</i>, too young to determine. <i>Sylvia borin</i>: Zaire — 1/0. Total: 15/4.</p>
<p>TIMALIIDAE. <i>Turdoides</i> sp.: Zaire — 1/1, <i>Leucocytozoon dubreuilii</i>.</p>
<p>TURDIDAE. <i>Cossypha heuglini</i>: Tanzania — 2/0. <i>Monticola saxitalis</i>: Kenya — 1/1, <i>Haemoproteus fallisi</i>. <i>Myrmecocichla aethiops</i>: Kenya — 6/1, <i>Leucocytozoon dubreuilii</i>. <i>Oenanthe oenanthe</i>: Kenya — 1/0. <i>Saxicola torquata</i>: Kenya — 3/1, <i>Haemoproteus fallisi</i>. <i>Turdus olivaceus</i>: Kenya — 2/1, <i>Trypanosoma avium</i>. <i>Zoothera oberlaenderi</i>: Tanzania — 1/1, microfilaria. Total: 16/5.</p>
<p>ZOSTEROPIDAE. <i>Zosterops virens</i>: Kenya — 1/1, <i>Haemoproteus zosteropi</i>.</p>

TABLE 2. Prevalence of hematozoa in three regions of Africa.

	Total examined	Number infected	Number of birds infected with					
			<i>Leuc.</i>	<i>Haemo.</i>	<i>Plasm.</i>	<i>Tryp.</i>	<i>Micro.</i>	Others
Kenya	279	53	20	28	9	4	2	
percent:		18.3	7	10	3	1.5	0.7	
Tanzania	306	144	50	49	24	6	10	27
percent:		47.0	16	16	8	2	3	9
Zaire	62	45	22	27	2	1	7	1
percent:		72.2	35	43	3	1.6	11	1.6
Total	647	242	92	104	35	11	19	28
percent:		37.2	14	16	5.4	1.7	2.9	4.3

The results (Tables 1, 2) indicate that blood parasites are widely distributed through a diverse avifauna in Kenya, Tanzania and Zaire, but their prevalence varies widely from region to region. Birds from Zaire were the most frequently parasitized, while those from Kenya were least frequently infected. The variability noted is undoubtedly due to such factors as the decade in which the sample was taken, sample size, time of year at which sample was taken, presence or absence of vectors in the various regions, vector feeding behavior in the different regions, etc., all factors known to affect prevalence. The variability is so great and the unknowns so numerous that no definitive conclusions can be drawn.

Possibly most interesting is the remarkably low prevalence of avian species of *Plasmodium*. Many authors will query the

validity of establishing prevalence of *Plasmodium* in a population on the basis of a single blood film diagnosis, and in view of the analogous experience with *Plasmodium* in human populations, such query is justified. Alternative forms of diagnosis, such as isodiagnosis, are simply not feasible, however, when applied to large scale avian blood parasite surveys. It is also true that single film diagnosis is similarly not conclusive for other blood parasites (a point frequently overlooked), but alternative methods of diagnosis, such as isodiagnosis, are biologically not applicable. Therefore, while the single film diagnostic technique may not present a complete picture of prevalence, it presents a valid comparative picture of the relative abundance of the different hematozoan species, particularly the haemosporidians.

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LITERATURE CITED

1. BENNETT, G. F. 1962. The hematocrit centrifuge for the laboratory diagnosis of hematozoa. *Can. J. Zool.* 40: 124-125.
2. DIAMOND, L. S. and C. M. HERMAN. 1954. Incidence of trypanosomes in the Canada Goose as revealed by bone marrow culture. *J. Parasit.* 40: 195-202.
3. TENDEIRO, J. 1947. Acerca dos hematozaires de algumas aves da Guine Portuguesa. *Rev. Med. Vet. (Lisboa)* 42: 285-350.
4. TRAVASSOS SANTOS DIAS, J. A. 1953. Resultados do um reconhecimento zoologico no Alto Limpopo efectuado pelos Drs. F. Zumpt e J. A. Travassos Santos Dias. *V. Hematozoarios das aves. Mocambique* 73: 61-99.

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