

REVIEW ARTICLE

Free-ranging avifauna as a source of generalist parasites for captive birds in zoological settings: An overview of parasite records and potential for cross-transmission

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ABSTRACT

Captive birds in zoological settings often harbor parasites, but little information is available about the potential for free-ranging avifauna to act as a source of infection. This review summarizes the gastrointestinal parasites found in zoo birds globally and in seven common free-ranging avian species [mallard (Anas platyrhynchos), Eurasian blackbird (Turdus merula), common starling (Sturnus vulgaris), Eurasian jackdaw (Corvus monedula), house sparrow (Passer domesticus), European robin (Erithacus rubecula), and rock dove (Columba livia)] to identify the overlap and discuss the potential for cross-species transmission. Over 70 references were assessed, and papers spanned over 90 years from 1925 to 2019. A total of 60 studies from 1987 to 2019 met the eligibility criteria. All examined free-ranging avifauna harbored parasite species that were also reported in zoo birds, except for the European jackdaw. Parasites reported in captive and free-ranging birds include nematodes (Capillaria caudinflata, Dispharynx nasuta, Ornithostrongylus quadriradiatus, Strongyloides avium, Syngamus trachea, and Tetrameres fissispina), cestodes (Dicranotaenia coronula, Diorchis stefanskii, Fimbriaria fasciolaris, and Raillietina cesticillus, Sobolevicanthus gracilis), trematode (Echinostoma revolutum), and protozoa (Cryptosporidium baileyi). Although no study effectively proved cross-transmission either experimentally or by genetic analysis, these parasites demonstrate low host specificity and a high potential for parasite sharing. There is potential for parasite sharing whenever determinants such as host specificity, life cycle, and husbandry are favorable. More research should be carried out to describe parasites in both captive and free-ranging birds in zoological settings and the likelihood of cross-infection. Such information would contribute to evidence-based control measures, enhancing effective husbandry and preventive medicine protocols.

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Introduction

Birds in zoological collections often harbor a variety of gastrointestinal parasites despite appropriate husbandry and veterinary care [1–3]. These parasites often cause disease in captive birds because confinement increases the risk of inter and intraspecific transmission, and sometimes high levels of stress may decrease the host's immune response [4–9].

Free-ranging birds are essential for ecosystem stability as they control insects and act as critical regulators in food chains, pollinators, seed dispersers, and scavengers [10]. However, they are also essential sources of parasites for a wide range of animal taxa, including humans and other mammals (e.g., *Cryptosporidium meleagridis* spread by Galliformes) [3,11]. The risk of parasite spillover from free living to captive birds in the zoological collection is possible

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in theory, but in practice it depends on parasite–host specificity, parasite life cycle, host resistance, husbandry-related factors, and environmental conditions [5,12,13].

The host specificity of parasites is variable. Some parasite species can affect a limited number of host species (also known as highly host-specific). On the contrary, others can be found in many host species, which are considered as generalists [14–16]. Parasite-sharing usually depends on the similarity of physiological characteristics among host species, which is likely to be higher in hosts that are closely related phylogenetically and/or share similar feeding habits, ecological niches, or geographic locations [14,17–21]. According to Rohde [22], a method to estimate parasite host specificity consists of the evaluation of "the number of host species from which the parasite has been collected." Other methods comprise the estimation of the variation in parasite infection levels among host species and the analysis of phylogenetic distinctiveness of hosts [13,14,22].

A vast amount of information is available about parasite taxa present in domestic and wild birds [15,23–37].

However, comparative studies that investigate the potential overlap of generalist parasites and cross-transmission between zoo birds and free-ranging avifauna are limited [38]. Understanding of which parasites occur in captive birds and free-ranging avifauna in zoological settings could provide insights into risks of transmission and help to establish effective prevention and control measures for zoological collections. The objectives of this systematic review are to identify the overlap between gastrointestinal parasite species reported in captive birds globally and those reported in seven common urban free-ranging bird species and to discuss the potential for cross-species transmission.

Materials and Methods

Database search

Relevant scientific documents were identified and reviewed following the Preferred Reporting Items for Systematic Reviews declaration guidelines (Fig. 1) [39]. We identified parasite species which have been reported in captive birds

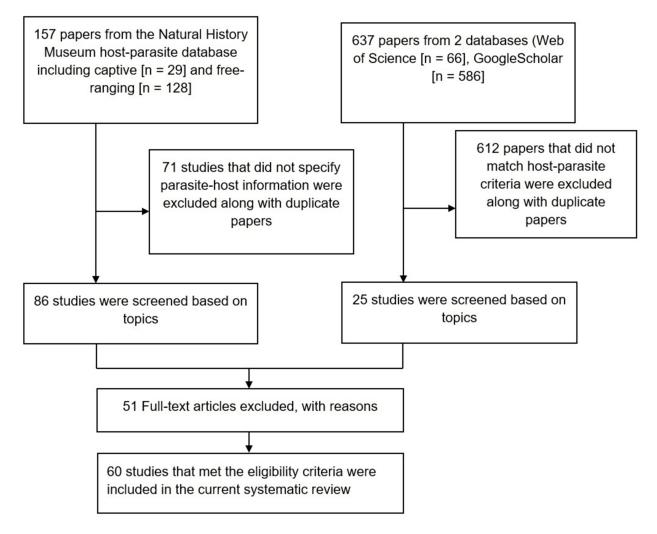


Figure 1. Flow diagram describing the study's design process.

and seven common free-ranging avian species using the Natural History Museum (NHM) London's host-parasite database (https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/ database/search.jsp) [40]. NHM is a compilation of references for parasites in many animal taxa and is available online [40]. Records of gastrointestinal helminths were identified (i.e., nematodes, cestodes, trematodes, and acanthocephalans) for birds listed in the categories "in captivity-zoo" and for seven cosmopolitan free-ranging avian species [i.e., mallard (Anas platyrhynchos), Eurasian blackbird (Turdus merula), common starling (Sturnus vulgaris), Eurasian jackdaws (Corvus monedula), European robin (Erithacus rubecula), house sparrow (Passer domesticus), and rock dove (*Columba livia*)] listed as "in the wild." Only those reports with parasites identified to full binomial species level were included in the study. Host and parasites identified to subspecies level were listed at the binomial species level instead [23]. Bird taxonomy was standardized according to the International Union for Conservation of Nature list [41]. Parasite names were standardized using the World Register of Marine Species database (http:// www.marinespecies.org), the tapeworm database at the University of Connecticut (http://tapewormdb.uconn. edu), and the Global Biodiversity Information Facility (www.gbif.org). Articles were categorized by geographical region (Asia, Africa, Australia, Europe, North America, and South America). Papers that assessed or discussed the transmission of parasites between captive and free-ranging birds in zoological conditions were identified for further review. Details about parasite prevalence, clinical and pathological signs, immunity, or pharmacological treatments were not considered in this study.

To identify more recent papers describing parasites of captive and free-ranging birds in zoological settings that have been excluded from the NHM database, we also conducted systematic searches on the Thompson Web of Science (https://webofknowledge.com/; 66 results; 26 February 2019) and Google Scholar (https://scholar. google.cl/; 586 results; 06 January 2020) using the following search terms: "parasites", and "intestinal", and "birds" and, "endo", and "gastro", or "captive", or "wild" or "Pigeon", or "Starling", or "Blackbird", or "Mallard", or "Robin", or "Jackdaw", or "House sparrow". Titles, abstracts, and/or full text were examined as necessary to determine whether the paper fit the inclusion criteria of reporting the transmission of endoparasites in zoo birds and free-ranging avifauna, with the full binomial species name, and clear host species described. From the phylum Protozoa, only reports on Apicomplexa, Isospora spp., Eimeria spp., and Cryptosporidium spp., were considered, and papers that assessed or discussed the transmission of parasites between captive and free-ranging birds were again identified for further review.

Data extractions and analysis

Extracted data included information about parasite species, host species, type of animal (captive or free-ranging), geographic location, authors, and year of publication. Data on endoparasites in captive and free-ranging birds were tabulated to determine parasite species overlap, according to host phylogenetic relationships. Results were displayed in Venn diagrams made using Visme (https://www.visme.co/).

Results and Discussion

Endoparasites of captive birds in zoological settings

After the exclusion criteria were applied, a total of 27 reports from 1987 to 2019 were identified for inclusion (Tables 1–3). Fifty-two parasite species were reported in 72 avian species in zoological settings, globally. Of a total of 27 studies, eight were carried out in Europe, six in Asia, five in North America, four in Africa, and four in South America.

Nineteen parasite families were identified in captive birds in zoological conditions, globally: Acuariidae, Amidostomatidae, Anisakidae, Cryptosporidiidae, Diplotriaenidae. Echinostomatidae. Eimeriidae, Habronematidae, Heterakidae, Hymenolepididae, Notocotylidae, Ornithostrongylidae, Renicolidae, Spiruridae, Strigeidae, Strongyloididae, Syngamidae, Tetrameridae, and Trichostrongylidae. Parasite species are shown in Tables 1-3.

Twenty-one parasites were reported in multiple avian species, with more than half of them reported (n=12) in Anseriformes. Five parasite species (i.e., *Aonchoteca longifilla*, *Capillaria caudinflata*, *Cyathostoma variegatum*, *Cryptosporidium parvum*, and *Cryptosporidium baileyi*) were found in two or more avian orders. *C. parvum* and *C. caudinflata* were identified as the most generalist parasites found in captive birds in zoological settings with reports in six and five different avian orders, respectively (*C. parvum* = Anseriformes, Galliformes, Psitaciformes, Craciformes, Pelecaniformes, and Columbiformes; *C. caudinflata* = Bucerotiformes, Galliformes, Pelecaniformes, Anseriformes, and Passeriformes).

Endoparasites in free-ranging birds

A total of 33 reports from 1987 to 2018 on endoparasites of mallard, Eurasian blackbird, common starling, Eurasian jackdaws, European robin, house sparrow, and rock dove were identified for inclusion. Seventeen of these studies were carried out in Europe, 11 in Asia, two in South America, one in North America, one in Africa, and one in Australia.

Fourteen parasite families and 54 parasite species were identified (Tables 1–3). *Ascaridia galli, Raillietina tetragona,*

Table 1. Nematodes reported in birds in zoological conditions globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow).

Parasite Family	Parasite	Host	^a Host Order	⁵Status	^c Location	Ref.
Acuariidae	C. obvelatus	Southern rockhopper penguin (Eudyptes chrysocome)	Sphe	С	SA	[69]
	D. nasuta	Golden-breasted starling (Lamprotornis regius)	Pass	С	NA	[70]
		House sparrow (P. domesticus)	Pass	F	SA	[71]
		Rock dove (C. livia)	Colu	F	AS, EU	[72-74]
	E. uncinata	Egyptian goose (Alopochen aegyptiaca)	Anse	С	EU	[75]
		Mallard (A. platyrhynchos)	Anse	С	EU	[75]
		Greylag goose (Anser anser)	Anse	С	EU	[75]
		Swan goose (A. cygnoides)	Anse	С	EU	[75]
		Bar-headed geese (Anser indicus)	Anse	С	EU	[75]
		Brent goose (Branta bernicla)	Anse	С	EU	[75]
		Red-breasted goose (Branta ruficollis)	Anse	С	EU	[75]
		Muscovy duck (C. moschata)	Anse	С	EU	[75]
		Black swan (C. atratus)	Anse	С	EU	[75]
		Black-necked swan (C. melancoryphus)	Anse	С	EU	[75]
		Mute swan (C. olor)	Anse	С	EU	[75]
		Common shelduck (T. tadorna)	Anse	С	EU	[75]
Amidostomatidae	Amidostomum anseris	Brent goose (B. bernicla)	Anse	С	EU	[75]
		Mute swan (C. olor)	Anse	С	EU	[75]
	Epomidiostomum anatinum	Mallard (A. platyrhynchos)	Anse	F	NA	[76]
	Epomidiostomum orispinum	Mute swan (<i>C. olor</i>)	Anse	С	EU	[75]
Ascarididae	Ascaridia columbae	Rock dove (C. livia)	Colu	F	AS, EU	[72–74,77
	A. galli	Rock dove (C. livia)	Colu	F	AS, EU	[72,74]
		House sparrow (P. domesticus)	Pass	F	AS	[78]
	A. platycerci	Fisher's lovebird (Agapornis fischeri)	Psit	С	EU	[79]
		Yellow-collared lovebird (<i>Agapornis</i> personatus)	Psit	С	EU	[79]
		Rosy-faced lovebird (Agapornis roseicollis)	Psit	С	EU	[79]
		Australian king-parrot (Alisterus scapularis)	Psit	С	EU	[79]
		Australian ringneck (Barnardius zonarius)	Psit	С	EU	[79]
		Yellow-crested cockatoo (<i>Cacatua</i> sulphurea)	Psit	С	EU	[79]
		Budgerigar (Melopsittacus undulatus)	Psit	С	EU	[79]
		Scarlet-chested parrot (<i>Neophema</i> splendida)	Psit	С	EU	[79]
		Eastern rosella (Platycercus eximius)	Psit	С	EU	[79]
		Red-rumped parrot (<i>Psephotus</i> haematonotus)	Psit	С	EU	[79]
		Rose-ringed parakeet (Psittacula krameri)	Psit	С	EU	[79]
	Porrocaecum	Eurasian blackbird (T. merula)	Pass	F	EU	[80]
	ensicaudatum	Common starling (S. vulgaris)	Pass	F	EU	[81]
		Eurasian jackdaw (C. monedula)	Pass	F	EU	[80]

Continued

Parasite Family	Parasite	Host	^a Host Order	⁵Status	^c Location	Ref.
Anisakidae	C. micropapillatum	Dalmatian pelican (<i>Pelecanus crispus</i>)	Pele	С	AS	[82]
Capillariidae	Aonchotheca exilis	Eurasian blackbird (T. merula)	Pass	F	EU	[83]
		Common starling (S. vulgaris)	Pass	F	EU	[80,83]
	A. longifilla	Yellow-billed chough (<i>Pyrrhocorax graculus</i>)	Pass	С	EU	[83]
		Northern red-billed hornbill (<i>Tockus</i> erythrorhynchus)	Buce	С	EU	[83]
	Baruscapillaria corvorum	House sparrow (P. domesticus)	Pass	F	EU	[84]
		Eurasian blackbird (T. merula)	Pass	F	EU	[84]
		Eurasian jackdaw (<i>C. monedula</i>)	Pass	F	EU	[84,85]
	Capillaria anatis	Northern pintail (Anas acuta)	Anse	С	EU	[75]
	C. anseris	Egyptian goose (Alopochen aegyptiacus)	Anse	С	EU	[75]
		Snow goose (Anser caerulescens)	Anse	С	EU	[75]
	C. caudinflata	Northern red-billed hornbill (<i>T. erythrorhynchus</i>)	Buce	С	EU	[83]
		Vulturine guineafowl (Acryllium vulturinum)	Galli	С	EU	[83]
		Asian crested ibis (N. Nippon)	Pele	С	AS	[45]
		Bar-headed geese (A. indicus)	Anse	С	EU	[75]
		House Sparrow (P. domesticus)	Pass	F	EU	[86]
		European robin (E. rubecula)	Pass	F	EU	[86]
		Eurasian blackbird (T. merula)	Pass	F	EU	[86]
		Common starling (S. vulgaris)	Pass	F	EU	[86]
	C. columbae	Rock dove (C. livia)	Colu	F	AS, EU	[72–74]
	Baruscapillaria obsignata	House sparrow (P. domesticus)	Pass	F	EU	[84]
		Rock dove (Columba liva)	Colu	F	AS, EU	[74,87,88]
	C. ovopunctata	Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[89]
		Common starling (S. vulgaris)	Pass	F	EU	[80]
		European robin (E. rubecula)	Pass	F	-	[86]
	C. resecta	Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[89]
		Eurasian jackdaw (<i>C. monedula</i>)	Pass	F	EU	[90]
		Eurasian jackdaw (<i>C. monedula</i>)	Pass	F	EU	[84]
	Eucoleus contortus	Eurasian wigeon (Mareca penelope)	Anse	С	EU	[75]
Diplotriaenidae	Dicheilonema rheae	Common emu (<i>Dromaius</i> novaehollandiae)	Stru	С	EU	[91]
		Greater rheas (Rhea americana)	Stru	С	AS	[82]
		Common ostrich (Struthio camelus)	Stru	С	EU	[91]
Habronematidae	Excisa buckleyi	White stork (Ciconia ciconia)	Cico	С	AS	[82]
	G. aspiculata	Orangequit (Euneornis campestris)	Pass	С	NA	[92]
		White-crested laughingthrush (Garrulax leucolophus)	Pass	С	NA	[92]
		White-spectacled bulbul (<i>Pycnonotus</i> xanthopygos)	Pass	С	NA	[92]
		Silver-throated tanager (<i>Tangara</i> icterocephala)	Pass	С	NA	[92]
		Harris's sparrows (Zonotrichia querula)	Pass	С	NA	[92]
	Hadjelia truncata	Rock dove (C. livia)	Colu	F	AS	[77]

Continued

Parasite Family	Parasite	Host	^a Host Order	bStatus	^c Location	Ref.
Heterakidae	Heterakis dispar	Snow goose (A. caerulescens)	Anse	С	EU	[75]
		Black-necked swan (<i>Cygnus</i> melanocoryphus)	Anse	С	EU	[75]
		Mute swan (C. olor)	Anse	С	EU	[75]
	H. gallinarum	Helmeted guineafowl (Numida meleagris)	Galli	С	AF	[93]
		Indian blue peafowl (Pavo cristatus)	Galli	С	AF	[93]
		Common pheasant (Phasianus colchicus)	Galli	С	AF	[93]
	Heterakis isolonche	Blue Eared Pheasant (<i>Crossoptilon</i> auritum)	Galli	С	EU	[94]
		Copper pheasant (Syrmaticus soemmerringii)	Galli	С	EU	[94]
		Brown eared pheasant (<i>Crossoptilon mantchuricum</i>)	Galli	С	EU	[94]
Ornithostrongylidae	O. quadriradiatus	Rock dove (C. livia)	Colu	C, F	AS, EU, SA	[87,88,95–98]
Strongyloididae	S. avium	Guinea fowl (N. meleagris)	Galli	С	AF	[46]
		Rock dove (C. livia)	Colu	F	EU	[96]
	Strongyloides pavoni	Peafowl (P. cristatus)	Galli	С	AF	[46]
Spiruridae	Paracyrnea yamagutii	Bar-headed geese (A. indicus)	Anse	С	AS	[99]
Syngamidae	C. variegatum	Mallard (A. platyrhynchos)	Anse	С	EU	[75]
		Snow goose (A. caerulescens)	Anse	С	EU	[75]
		Bar-headed geese (A. indicus)	Anse	С	EU	[75]
		Black swan (C. atratus)	Anse	С	EU	[75]
		Common emu (D. novaehollandiae)	Stru	С	NA	[100]
	S. trachea	House sparrow (P. domesticus)	Pass	F	EU	[101]
		Bar-headed geese (A. indicus)	Anse	С	EU	[75]
Tetrameridae	Tetrameres americana	Greater prairie chicken (<i>Tympanuchus</i> cupido)	Galli	С	NA	[102]
	T. fissispina	Eurasian wigeon (M. penelope)	Anse	С	EU	[75]
		Mallard (A. platyrhynchos)	Anse	C, F	EU, NA	[75,76]
		Rock dove (C. livia)	Colu	F	EU, AS	[74,87,103]
Trichostrongylidae	Trichostrongylus tenuis	Mute swan (C. olor)	Anse	С	EU	[75]

^aAnse = Anseriformes; Buce = Bucerotiformes; Craci = Craciformes; Cico = Ciconiiformes; Colu = Columbiformes; Galli = Galliformes; Passe = Passeriformes; Pele = Pelecaniformes; Pici = Piciformes = Psittaciformes; Sphe = Sphenisciformes; Stri = Strigiformes; Stru = Struthioniformes. ^bC = Captivity; F = Free-ranging.

and *Raillietina echinobothrida* were the most generalist parasites affecting Passeriformes and Columbiformes.

Endoparasite species found in both zoo birds and free-ranging avifauna

Of a total of 102 parasite species reported in zoo birds and free-ranging avifauna, only 13 parasite species were reported in both captive and free-ranging birds (Tables 1–3) (Figs. 2–5).

Parasite species that were reported in zoo birds and free-ranging avifauna include nematodes (*C. caudinflata*,

Dispharynx nasuta, Ornithostrongylus quadriradiatus, Strongyloides avium, Syngamys trachea, and Tetrameres fissispina), cestodes (Dicranotaenia coronula, Diorchis stefanskii, Fimbriaria fasciolaris, Raillietina cesticillus, and Sobolevicanthus gracilis), trematodes (Echinostoma revolutum), and protozoa (C. baileyi). When considering parasite findings in relation to geographic location, 8 of the 13 parasite species in zoo birds and free-ranging avifauna (i.e., C. caudinflata, S. trachea, T. fissipina, D. coronula, O. quadriradiatus, F. fasciolaris, S. gracilis, and D. stefanskii) were reported in Europe; R. cesticillus in Asia; and C. baileyi in

^cSA = South America; NA = North America; EU = Europe; AF = Africa; AS = Asia.

Table 2. Cestodes, trematodes, and acanthocephalans reported in birds in zoological conditions globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow).

Parasite Family	Parasite	Host	^a Host Order	bStatus	^c Location	Ref.
Cestodes						
Anoplocephalidae	Aporina delafondi	Rock dove (C. livia)	Colu	F	EU	[74]
Davaineidae	Cotugnia polyacantha	Rock dove (C. livia)	Colu	F	AS	[72]
	C. satpuliensis	Rock dove (C. livia)	Colu	F	AS	[72]
	C. columbae	Rock dove (C. livia)	Colu	F	AS	[72]
	C. digonoporta	Rock dove (C. livia)	Colu	F	AS	[72]
	R. cesticillus	Rock dove (C. livia)	Colu	C, F	AS	[88,104]
	R. bonini	Rock dove (C. livia)	Colu	F	AS	[72]
	R. carpohagi	Rock dove (C. livia)	Colu	F	AS	[72]
	R. echinobothrida	Rock dove (C. livia)	Colu	F	AS	[73,77]
		House sparrow (P. domesticus)	Pass	F	AS	[78]
	R. galeritae	House sparrow (P. domesticus)	Pass	F	AS	[78]
	R. fuhrmani	Rock dove (C. livia)	Colu	F	AS	[72]
	R. magninumida	Rock dove (C. livia)	Colu	F	AS	[73,77]
	R. micracantha	Rock dove (C. livia)	Colu	F	EU	[74]
	R. tetragona	Rock dove (C. livia)	Colu	F	AS	[72,73]
		House sparrow (P. domesticus)	Pass	F	AS	[78]
Dilepididae	Anomotaenia constricta	Eurasian jackdaw (C. monedula)	Pass	F	EU	[85]
	Choanotaenia infundibulum	House sparrow (P. domesticus)	Pass	F	AS	[78]
	Dilepis undula	Eurasian blackbird (T. merula)	Pass	F	EU	[105]
		Common starling (S. vulgaris)	Pass	F	EU	[80]
		Eurasian jackdaw (C. monedula)	Pass	F	EU	[80]
Hymenolepididae	Cloacotaenia megalops	Brent goose (B. bernicla)	Anse	С	EU	[75]
	D. coronula	Mallard (A. platyrhynchos)	Anse	C, F	EU	[75,106]
		Muscovy duck (C. moschata)	Anse	С	EU	[75]
		Upland goose (C. picta)	Anse	С	EU	[75]
		Black swan (<i>C. atratus</i>)	Anse	С	EU	[75]
	Diorchis elisae	Common Pochard (Aythya ferina)	Anse	С	EU	[75]
	D. stefanskii	Mute swan (<i>C. olor</i>)	Anse	С	EU	[75]
	-	Mallard (A. platyrhynchos)	Anse	F	EU	[106]
	Drepanidotaenia lanceolate	Mallard (A. platyrhynchos)	Anse	С	EU	[75]
	•	Brent goose (B. bernicla)	Anse	С	EU	[75]
		Black swan (<i>C. atratus</i>)	Anse	С	EU	[75]
		White-faced Whistling-duck (Dendrocygna viduata)	Anse	С	EU	[75]
	F. fasciolaris	Mallard (A. platyrhynchos)	Anse	C, F	EU, NA	[75,76]
		Upland goose (C. picta)	Anse	С	EU	[75]
		Mute swan (C. olor)	Anse	С	EU	[75]
	Hymenolepis Columbae	Rock dove (C. livia)	Colu	F	EU	[74]
	Hymenolepis echinocotyle	Northern shoveler (Anas clypeata)	Anse	С	EU	[107]
	Microsomacanthus	Mallard (A. platyrhynchos)	Anse	С	EU	[75]
	paracompressa	Mute swan (C. olor)	Anse	С	EU	[75]
	Parabisaccanthes philactes	Mute swan (C. olor)	Anse	С	EU	[75]
	S. gracilis	Mallard (A. platyrhynchos)	Anse	C, F	EU	[75,106]
		Muscovy duck (C. moschata)	Anse	С	EU	[75]
		Upland goose (C. picta)	Anse	С	EU	[75]
		Black swan (C. atratus)	Anse	С	EU	[75]
		Mute swan (C. olor)	Anse	С	EU	[75]
		Common shelduck (<i>T. tadorna</i>)	Anse	С	EU	[75]
	Sobolevicanthus columbae	Rock dove (<i>C. livia</i>)	Colu	F	EU	[74]
	Tschertkovilepis setigera	Mallard (A. platyrhynchos)	Abse	С	EU	[75]
	. 3	Bar-headed geese (A. indicus)	Anse	C	EU	[75]
		Brent goose (B. bernicla)	Anse	C	EU	[75]
		Mute swan (<i>C. olor</i>)	Anse	С	EU	[75]

Continued

Parasite Family	Parasite	Host	^a Host Order	⁵Status	^c Location	Ref.
Trematode						
Cyclocoelidae	Morishitum vagum	Eurasian blackbird (T. merula)	Pass	F	AS	[108]
Dicrocoeliidae	Brachydistomun ventricosum	House sparrow (P. domesticus)	Pass	F	EU	[109]
		Eurasian blackbird (T. merula)	Pass	F	AS	[109]
		Common starling (S. vulgaris)	Pass	F	EU	[109]
	Lutztrema attenuatum	Eurasian blackbird (T. merula)	Pass	F	EU	[110]
		Common starling (S. vulgaris)	Pass	F	EU	[111]
Brachylaimidae	Brachylaemus columbae	Rock dove (C. livia)	Colu	F	EU	[74]
	Brachylecithum mosquensis	European robin (E. rubecula)	Pass	F	EU	[109]
		Common starling (S. vulgaris)	Pass	F	EU	[112]
	Brachylaima fuscatus	Common starling (S. vulgaris)	Pass	F	EU	[80]
		Eurasian jackdaw (C. monedula)	Pass	F	EU	[111]
Echinostomatidae	Chaunocephalus ferox	White stork (C. ciconia)	Cico	С	AS	[82]
	E. revolutum	Painted stork (Mycteria leucocephala)	Cico	С	AS	[98]
		House sparrow (P. domesticus)	Pass	F	SA	[113]
Notocotylidae	Catatropis verrucosa	Mute swan (C. olor)	Anse	С	EU	[75]
Plagiorchiidae	Plagiorchis elegans	Common starling (S. vulgaris)	Pass	F	EU	[80]
	Plagiorchis maculosus	House sparrow (P. domesticus)	Pass	F	EU	[80]
		Common starling (S. vulgaris)	Pass	F	EU	[80]
Prosthogonimidae	Prosthogonimus ovatus	House sparrow (P. domesticus)	Pass	F	EU	[80]
Renicolidae	Renicola heroni	Goliath heron (Ardea goliath)	Pele	С	AF	[114]
Strigeidae	Apharyngostrigea simplex	Snowy egret (<i>Egretta thula</i>)	Pele	С	SA	[115]
Acantocephala	. , , , , , , , , , , , , , , , , , , ,	, , ,				
Plagiorhynchidae	Plagiorhynchus cylindraceus	European robin (E. rubecula)	Pass	F	EU	[116]
o ,	<i>3</i> , ,	House sparrow (<i>P. domesticus</i>)	Pass	F	EU	[116]
		Eurasian Blackbird (<i>T. merula</i>)	Pass	F	AU	[117]
		Common starling (S. vulgaris)	Pass	F	AU, EU	[117,118]
		Eurasian Jackdaw (<i>C. monedula</i>)	Pass	F	EU	[80]
	Plagiorhynchus gracilis	Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[116]
	3 , 3	Common starling (S. vulgaris)	Pass	F	EU	[116]
		European robin (<i>E. rubecula</i>)	Pass	F	EU	[116]
	Prosthorhynchus transversus	Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[80]
	,	Common starling (S. vulgaris)	Pass	F	EU	[80]
Polymorphidae	Corynosoma constrictum	Mallard (<i>A. platyrhynchos</i>)	Anse	F	NA	[76]
Gigantorhynchidae	Mediorhynchus micracanthus	Common starling (<i>S. vulgaris</i>)	Pass	F	EU	[116]
	,,	House sparrow (<i>P. domesticus</i>)	Pass	F	EU	[116]
		Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[116]
	Mediorhynchus papillosus	House sparrow (<i>P. domesticus</i>)	Pass	F	SA	[71]
	,	Eurasian jackdaw (<i>C. monedula</i>)	Pass	F	EU	[116]
Centrorhynchidae	Sphaerirostris turdi	Eurasian blackbird (<i>T. merula</i>)	Pass	F	EU	[116]
Seria orny nemade	apriderii ostris turui	Common starling (S. vulgaris)	Pass	F	EU	[116]

^aAnse = Anseriformes; Buce = Bucerotiformes; Craci = Craciformes; Cico = Ciconiiformes; Colu = Columbiformes; Galli = Galliformes; Passe = Passeriformes; Pele = Pelecaniformes; Pici = Piciformes = Psittaciformes; Sphe = Sphenisciformes; Stri = Strigiformes; Stru = Struthioniformes. ^bC = Captivity; F = Free-ranging.

Africa. *D. nasuta, S. avium,* and *E. revolutum* were identified in reports in zoo birds and free-ranging avifauna located on different continents.

All examined free-ranging avifauna harbored parasite species that have been reported in zoo birds, except for the Eurasian jackdaw. In this species, only morphological evidence of *Capillaria* sp. ova was available [42]. (see Tables 1–3).

There is limited evidence for the transmission of gastrointestinal parasites from free-ranging avifauna to zoo birds in the literature. Few studies have carried out experimental procedures or statistical analyses to prove the cross-transmission of parasites between captive and free-ranging individuals [43,44]. The majority of recent studies simply describe parasites in fecal samples or on postmortem examination [27,45–47]. This review

cSA = South America; NA = North America; EU = Europe; AF = Africa; AS = Asia.

Table 3. *Eimeria* spp., *Isospora* sp., and *Cryptosporidium* spp. reported in birds in zoological conditions globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow).

Parasite Family	Parasite	Host	^a Host Order	⁵Status	^c Location	Ref.
Eimeriidae	Eimeria mutica	Indian peafowl (P. cristatus)	Galli	С	AF	[46]
	E. pavonis	Indian peafowl (P. cristatus)	Galli	С	AF	[46]
	E. pavoniva	Indian peafowl (P. cristatus)	Galli	С	AF	[46]
	E. mayurai	Indian peafowl (P. cristatus)	Galli	С	AF, AS	[46,98]
	E. mandali	Indian peafowl (P. cristatus)	Galli	С	AF	[46]
	E. abmitu	Razor-billed curassow (Mitu tuberosum)	Galli	С	SA	[119]
	E. amazonae	Blue-fronted amazon (Amazona aestiva)	Psit	С	SA	[119]
	E. forresteri	Toco toucans (Ramphastos toco)	Pici	С	SA	[119]
	E. labbeana	Rock dove (C. livia)	Colu	F	AS	[72,98,120]
	E. kapotei	Rock dove (C. livia)	Colu	F	AS	[120]
	E. columbae	Rock dove (C. livia)	Colu	F	AS	[120]
	Isospora aegyptia	House sparrow (P. domesticus)	Pass	F	AS	[78]
	Isospora lacazei	House sparrow (P. domesticus)	Pass	F	AS	[121]
	Isospora lusitanensis	Eurasian blackbird (T. merula)	Pass	С	EU	[122]
Cryptosporidiidae	C. parvum ^d	Black swan (C. atratus)	Anse	С	AS	[65]
		Malay Crestless fireback (Lophura erythrophthalma)	Galli	С	AS	[65]
		Fischer's lovebird (A. fischeri)	Psit	С	AS	[65]
		Gorlden pheasant (Chrysolophus pictus)	Galli	С	AS	[65]
		Great Argus pheasant (Argusianus argus)	Galli	С	AS	[65]
		Great curassow (Crax rubra)	Craci	С	AS	[65]
		Pink backed pelican (Pelecanus rufescens)	Pele	С	AS	[65]
		Rock dove (C. livia)	Colu	С	SA	[123]
	C. baileyi	Ring-necked pheasant (P. colchicus)	Galli	С	AF	[3]
		Snowy owl (Bubo scandiacus)	Stri	С	AS	[124]
		Mallard (A. platyrhynchos)	Anse	F	AF	[3]
	C. hominis	Rock dove (C. livia)	Colu	F	EU	[125]
	C. meleagridis	Mallard (A. platyrhynchos)	Anse	F	AF	[126]

^aAnse = Anseriformes; Buce = Bucerotiformes; Craci = Craciformes; Cico = Ciconiiformes, Colu = Columbiformes, Galli = Galliformes; Psit = Psittaciformes, Stri = Strigiformes. ^bC = Captivity; F = Free-ranging. ^cAF = Africa; AS = Asia; EU = Europe; NA = North America; SA = South America. ^dBirds are accidental carriers of *C. parvum*.

identifies parasite species that have been reported in both zoo birds and free-ranging avifauna. This information may be useful to highlight common parasites of zoo birds, for which free-ranging birds may be the source. In the following section, we discuss various factors involved in the transmission of generalist gastrointestinal parasites from free-ranging avifauna to captive birds, including parasite-host specificity, host range, parasite life cycle, and husbandry protocols [5,12,13,18]. Discussion of host resistance is beyond the scope of this review.

Host range and specificity

In this review, *C. caudinflata, D. nasuta, O. quadriradiatus, S. avium, S. trachea, T. fissispina, D. coronula, D. stefanskii,*

E. fasciolaris, R. cesticillus, S. gracilis, E. revolutum, and *C. baileyi* were reported in several avian orders under both captive and free-ranging conditions, which indicates relatively low host specificity. Free-ranging birds could become a source of infection with these parasite species if they share the same geographical location as a phylogenetically closely related zoo bird. This is of particular significance for zoo birds maintained in outdoor exhibits where they are likely to be exposed to feces from free-ranging birds. Most of the reports we reviewed based their diagnosis on morphology and morphometric evaluation, and none of them proved effective cross-species transmission. To confirm that a parasite shows low host specificity, it has to be subjected to genetic analysis and/or

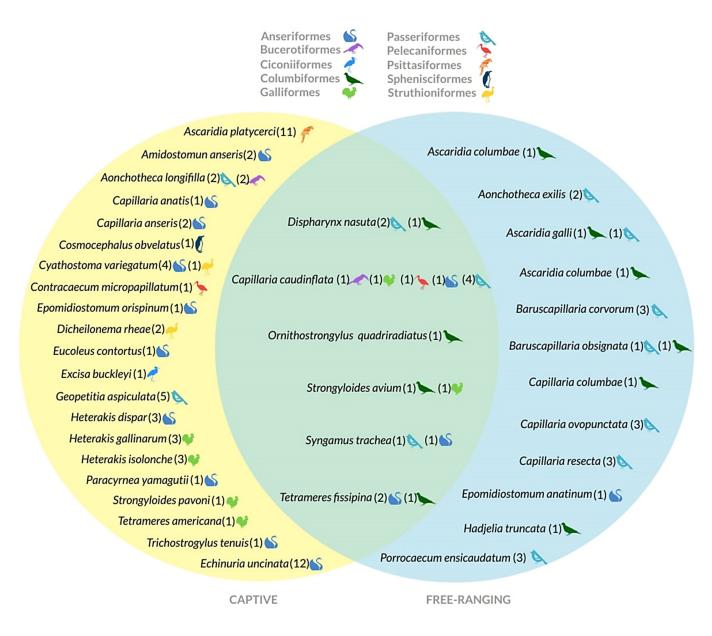


Figure 2. Overlap of nematodes reported in zoo birds globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow). Parentheses () show the number of bird species in each avian order.

experimental transmission studies, since cryptic species might have indistinguishable morphotypes [13,48,49]. For example, one experiment demonstrated that parasite-free chickens acquired *Ascaris lineata* and *Heterakis gallinarum* infections due to exposure to free-ranging birds such as Eurasian black birds, confirming actual rather than potential overlap [50]. In Bristol Zoo Gardens in the UK, Carrera-Jativa et al. [42] suggested potential parasite sharing of capillarids between closely related species such as captive Asian Azure-winged magpies

(*Cyanopica cyanus*) and wild Eurasian jackdaws based on overlap in egg morphology using the Mini-FLOTAC coprological method and the Principal Component Analysis statistical test. However, they did not isolate adult parasite specimens or carry out infection trials or molecular tests to confirm cross-infection.

In contrast to the situation with nematodes, in this review, captive and free-ranging avian species that harbored the same cestode species were more closely phylogenetically related to each other than species with the same

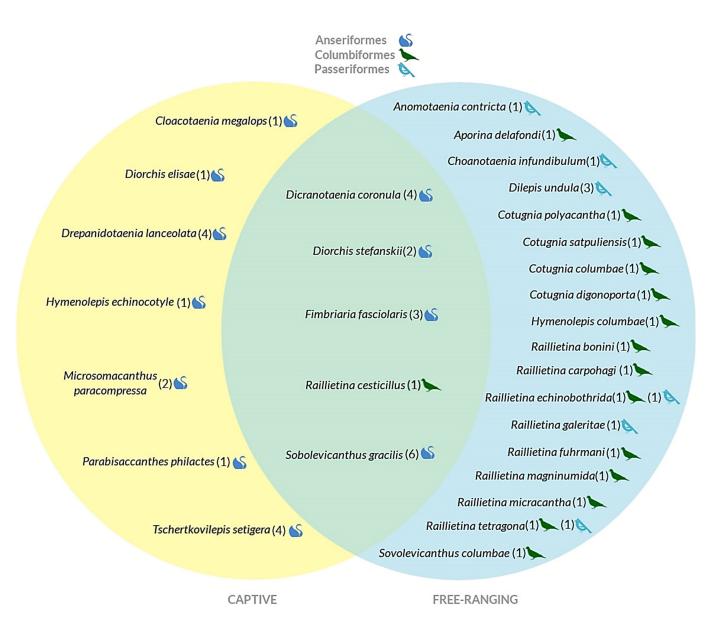


Figure 3. Overlap of cestodes reported in zoo birds globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow). Parentheses () show the number of bird species in each avian order.

nematode species. This is in accordance with the literature, which suggests higher host specificity among avian cestodes [13,23,48]. For instance, *D. coronula* and *S. gracilis* were only found in Anseriformes [i.e., mallard, muscovy duck (*Cairina moschata*), upland Goose (*Chloephaga picta*), black swan (*Cygnus atratus*), mute Swan (*Cygnus olor*), and common shelduck (*Tadorna tadorna*)] and not in other species whose diet include fish. Nevertheless, overlap and cross-transmission of cestodes between bird species in the same order appear to be common.

Parasite life cycles

Some parasites that were reported in zoo birds and free-ranging avifauna are species with direct life cycles (e.g., *Heterakis* spp., *Syngamus* spp., some capillarids, orders Rhabditoidea, Strongyloidea, and Trichostrongyloidea). On the contrary, other parasite species have indirect life cycles (e.g., *Cosmocephalus obvelatus*, *D. nasuta*, *Echinuria uncinata*, *Contracaecum micropapillatum*, *Geopetitia aspiculata*, *T. fissispina*, *Tetrameres americana*, cestodes, trematodes, and acanthocephalans) [23,46,51].

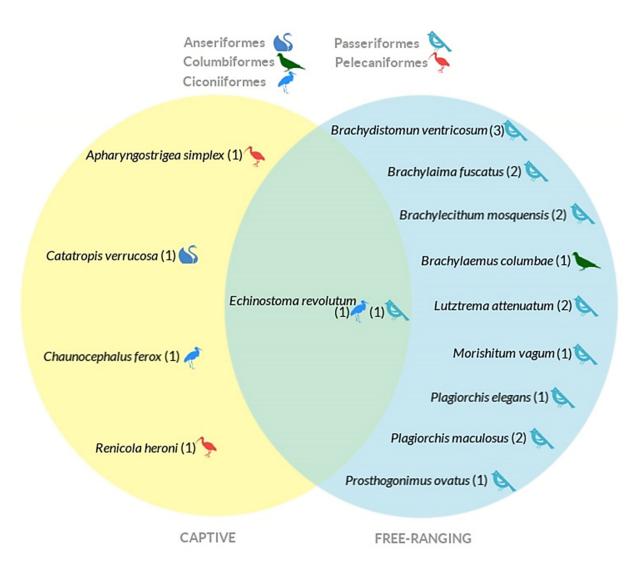


Figure 4. Overlap of trematodes reported in zoo birds globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow). Parentheses () show the number of bird species in each avian order.

Direct life cycles

Overall, monoxenous parasites that show direct life cycles require a single host to develop sexual maturity [23]. Parasite eggs of nematodes and non-sporulated oocysts of coccidia are shed in feces by the infected hosts, and they become infective in the environment by different biological processes, such as larval development and molting (nematodes) or sporogony (coccidia) [23]. Free-living larvae of strongylid nematodes require optimal environmental conditions to remain viable [23]. However, some parasites can resist extreme temperatures for long periods, such as ascarids [52]. Animals can be infected with

monoxenous parasites by eating infective larval stages, eggs, or oocysts available in contaminated food, water, or soil [52]. Also, some birds become infected by eating invertebrates, which act as transport hosts for monoxenous parasites (e.g., earthworms for *A. galli*) [53]. In the new hosts, parasitic elements complete their development by migrating to the gastrointestinal tract where they reproduce sexually (nematodes) or asexually/sexually (coccidia) [23].

Monoxenous parasites are essential in zoos because fecal-oral transmission can occur easily [23]. Captive birds can also become continually reinfected by the ingestion of contaminated food or soil, which will raise

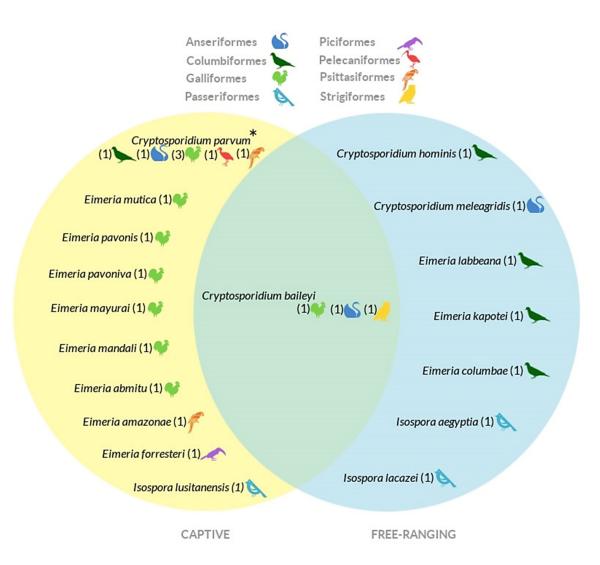


Figure 5. Overlap of coccidia reported in zoo birds globally and in seven cosmopolitan urban free-ranging birds (mallard, rock dove, common starling, Eurasian jackdaw, Eurasian blackbird, European robin, and house sparrow). Parentheses () show the number of bird species in each avian order. * Birds are accidental carriers of *C. parvum*.

their parasite burden and cause more severe pathological conditions [11,23,54]. One experiment in poultry proved that birds infected with gastrointestinal parasites became the source of infection for others [50]. Indeed, reinfection with *A. galli* in commercial laying hens took place 7 days after the administration of the anthelmintic flubendazole in controlled environments [55]. Zoo birds housed in outdoor aviaries are likely exposed to contaminated feces from free-ranging birds harboring generalist monoxenous parasites. Although captive animals may already be infected with endoparasites, the exposure to contaminated feces of free-ranging birds can contribute to their parasitism [50]. Therefore, there is a risk of

transmission of generalist monoxenous parasites from free-ranging avifauna to compatible zoo birds (see Tables 1–3) (see Figs. 2–5).

Indirect life cycles

Ten of the documented helminth species such as *D. nasuta, C. micropapillatum, G. aspiculata, Tetrameres fissipina, C. caudinflata, D. coronula, D. stefanskii, F. fasciolaris, S. gracilis, and E. revolutum) have an indirect life cycle (Tables 1–3). Heteroxenous parasites, which have an indirect life cycle, require at least one intermediate host to complete their development [23]. In general, heteroxenous parasites include some nematodes,*

digenetic trematodes, cestodes, and acanthocephalans [23]. Vertebrates (e.g., fish and amphibians) and invertebrates (e.g., earthworms, arthropods, and mollusks) can be intermediate hosts of heteroxenous parasites, which depend on the particular parasite species and the definitive host's diet [23]. Free-living developmental stages, such as larvae or larvated eggs, require favorable environmental conditions to remain viable until they find a suitable intermediate host [23]. The degree of dependence on such conditions varies for each parasite taxa. For example, free-living larvae of digenetic trematodes require on moderate temperatures while cestode eggs can survive even on freezing conditions [56,57]. Definitive avian hosts become infected only if intermediate hosts are available in the environment [23].

The significance of heteroxenous parasites in zoological settings depends upon environmental conditions and the presence or absence of intermediate hosts. Exposure to feces from infected free-ranging avifauna does not result in the transmission of generalist parasites, and new cases can be controlled if intermediate hosts are identified and eliminated [58,59].

Biological vectors and carriers

Although a given parasite species might be unable to infect a bird species due to host incompatibility, it may be spread by free-ranging avifauna acting as accidental carriers [23]. In particular, free-ranging birds could spread viable parasitic forms through material carried on their feet, beak, or plumage, especially to zoo birds in naturalistic enclosures with open access to free-ranging birds [50,60]. Also, some birds can mechanically spread infective parasite eggs or oocysts from one location to another by eating contaminated food and then shedding viable parasitic forms in their feces [61–63]. For example, migratory Anseriformes can shed infective C. parvum oocysts between locations by acting as mechanical vectors [63]. Furthermore, in Ohio and Illinois, it was concluded that Canada Geese (Branta canadensis) were accidental carriers for zoonotic Cryptosporidium spp., such as C. parvum and C. hominis, but natural reservoirs for C. goose genotype I and C. goose genotype II [61]. As contaminated water is the primary source for transmission of zoonotic strains among animals, according to Zhou et al. [61], it is likely that zoological parks with naturalistic exhibits containing ponds accessible to free-ranging birds may risk transmission of pathogenic strains for their birds or other animals [11,61,63,64]. Many studies on the presence of cryptosporidiosis in zoo birds have been carried out, but few of them were able to identify *Cryptosporidium* to the taxonomic species level [11,65,66]. In the Kuala Lumpur Zoo in Malaysia, *C. parvum* was detected by staining and molecular methods in fecal samples from six orders of captive birds (Anseriformes, Buceriformes, Craciformes, Galliformes, Pelecaniformes, and Psittaciformes; frequency = 9%) and in different enclosures [65]. Quah et al. [65] suggested that although the specific strain found was not dangerous to the aviary, it could be transmitted to people. The source of infection in this case and infection acquired before or during captivity was not described. Hence, the likelihood that free-ranging avifauna was the source of infection for captive birds or vice versa cannot be rejected.

Therefore, in zoological settings, it is possible that free-ranging birds transmit certain endoparasites to captive individuals through exposure to their feces or to materials attached to their bodies even if they are not the natural host for the parasite species.

Husbandry

The high incidence of infections involving generalist parasites in captive avian collections demands careful inspection of husbandry protocols. In the Columbus Zoo, U.S., captive and free-ranging birds were reported to harbor a variety of endoparasites [43]. Faust & Pappas [43] associated high prevalence and diversity of parasitism with more naturalistic exhibits containing ponds and vegetation. Parasites were found both in open enclosures with access to free-ranging avifauna and in outdoor aviaries housing different avian species. Only birds located in indoor and sanitary-controlled conditions were free from any kind of parasite. Later, in the same zoological park, fecal samples from free-ranging waterfowls were collected to investigate the presence of potential pathogens for both zoo animals and people [44]. Wild Canada geese (Branta canadensis), mallards, and domestic hybrid species were reported to be infected with some nematodes (e.g., ascarids, capillarids, spirurids, and strongylids) and coccidia. Fallacara et al. [44] concluded that congregations of free-ranging waterfowls in the zoo could jeopardize the health of captive animals and people due to the potential for transmission of the pathogenic bacteria identified (e.g., Salmonella spp., Escherichia coli, and Campylobacter jejuni). Information about parasites present in the captive birds was not provided. This could have indicated the possibility of parasite cross-transmission between birds from related taxa. Since feces of free-ranging birds may contaminate enclosures, especially outdoor exhibits, control of exposure of captive birds might need to be reduced, e.g., by removing nearby roosts. Replacement of contaminated substrates and/or complete habitat disinfection may be essential to minimize reinfection in affected birds [67].

Finally, zoo birds may become infected with gastrointestinal parasites by several other routes, including from contaminated food and other materials acting as fomites [68]. In captive breeding centers in China, more than half of Asian crested ibis (Nipponia Nippon) were positive for Ascaris spp. and C. caudinflata by coprological examination [45]. Zhang at al. [45] concluded that birds themselves were a source of secondary infection due to the presence of parasite eggs in feces, and primary infections were associated with the provision of contaminated food (i.e., mudfish acting as mechanically carriers for Ascaris sp.). Thus, preventative husbandry measures should include food inspection and additional biosecurity measures. Also, a well-defined program of anti-parasite treatment may still be necessary to reduce the parasite burden.

Conclusion

Exposure to free-ranging avifauna may result in parasite infection of zoo birds if parasite-host specificity and environmental conditions for parasitic development are suitable. Phylogenetic closeness, similar feeding habits and/or the same geographical distribution are the primary determinants for the host range of a parasite, as well as parasite taxon (e.g., nematode versus cestode). Generalist parasite species that tolerate differences in host physiology can infect a large variety of avian species. Developmental stages of all parasites require either suitable environmental conditions or/and the presence of intermediate host to conclude their life cycle in definitive avian hosts. In zoological settings, captive birds may be infected with generalist gastrointestinal monoxenous parasites such as *S. trachea*. They may become directly infected by eating materials contaminated with the feces of free-ranging avifauna, and they become reinfected by eating food or feeding off substrates contaminated with their own feces. Generalist heteroxenous parasites are more likely to occur in zoo birds housed in more naturalistic exhibitors as they require both suitable environmental conditions and the availability of intermediate hosts to complete their development.

There are few studies demonstrating direct evidence of the actual transmission of endoparasites in zoos. More research should be carried out to describe the parasite species affecting both captive and free-ranging birds in zoological settings and their cross-species transmission. The present study provides useful information about generalist endoparasites present in zoo birds and seven cosmopolitan urban free-ranging birds. This information will be beneficial for further epidemiological studies and the establishment of evidence-based control measures.

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Conflict of interest

The authors declare that they have no conflict of interests.

Authors' contribution

Conceptualization was done by PDCJ and ERM. Methodology and data collection were carried out by PDCJ. Writing: the original draft was done by PDCJ, and preparation and critical checking were carried out by PDCJ, MB, ERM, and GJU. Supervision was done by JRAT.

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