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The effect of host foraging ecology on the prevalence and intensity of coccidian infection in wild passerine birds

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The prevalence and intensity of infection with isosporan Coccidia parasites in wild passerine birds varies greatly between bird species. Faeces of infected hosts contain oocysts that are a source of new infections when ingested. As a consequence, we expect that the main route of coccidiosis transmission in the wild is related to the foraging behaviour of the hosts, and that bird species are exposed to infective oocysts, depending upon the way of foraging. We studied how prevalence and intensity of isosporan infection in wild birds are related to foraging stratum, gregariousness, and diet. Our data reveal that a bird's feeding habits play a significant role in the extent and severity of infection by isosporan Coccidia in the wild.

Key words: avian diseases, host–parasite relationships, songbirds, *Isospora* spp., Coccidia, foraging ecology

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Wild birds are infected with a variety of parasites, including ectoparasites, intestinal parasites, and blood parasites. Parasites can affect various aspects of the host's life history (Milinski 1990, Tella *et al.* 2002, Buchholz 2004, Marzal *et al.* 2005). However, the mechanisms and routes of infection are poorly understood, in particular amongst non-vector borne parasites that may obtain infection from different sources like those causing coccidiosis. Coccidia are deleterious intestinal protozoan parasites that are wide-spread among domestic and wild birds. They can cause reduced weight gain, affect intestinal nutrient resorption, reduce fertility, or impact carotenoid-based plumage coloration (Long 1982, Buchholz 2004). Passerine birds are mainly infected by Coccidia of the genus *Isospora* (Apicomplexa: Coccidiida) (e.g. Svobodová 1994). Avian Coccidia are transmitted via oocysts that are excreted with the faeces of the host, usually in the late afternoon (Boughton 1933, Schwalbach 1960, Dolnik 1999a,b, Misof 2004, López *et al.* 2007), and sporulation takes 2–6 days. Before becoming infective, oocysts must sporulate under appropriate conditions. Transmission occurs when a foraging bird ingests the sporulated oocysts. Consequently, infection in wild birds is likely to depend on where birds forage and what they eat. We addressed this subject by correlating the prevalence and intensity of *Isospora* infection in a set of more than 700 faecal samples of 37 wild European passerine bird species and compared these findings with the foraging habits of the birds.

METHODS

The study was conducted at the Biological Station Rybachy on the Baltic Sea coast (Curonian Spit, Russia; 55°09'14"N 20°51'33"E) in late summer and early autumn 1995–1999. Birds were captured with mist nets, ringed, and processed following the guidelines of the ESF-programme (Bairlein 1995). Recorded data included the date, time of capture, species, and age of the bird.

The intensity of Coccidia infection rapidly decreases with the host's age (Dolnik 1998, 2002). Therefore, only juvenile birds were considered in the analysis. Moreover, due to the diurnal variation in *Isospora* oocysts output (e.g. Dolnik 1999b, Misof 2004) only

birds caught between 16:00 and 18:00 were considered in this analysis. In total, 721 juvenile birds of 37 passerine species were sampled (Table 1).

Following capture and ringing, the birds were kept for 5–15 min in small individual cages with clean ground paper and then released. A fresh droplet of faeces from each individual bird was placed in an individually labelled tube with 2% $K_2Cr_2O_7$ aqueous solution. In the lab, the samples were kept for a week at room temperature to allow the oocysts to sporulate. Flotation in saturated NaCl solution was used to concentrate the oocysts (for details see Dolnik 2006). Each sample was shaken well and put into 10 ml centrifuge-tube topped up to 10 ml volume with water. The sample was centrifuged for 5 min at 1500 RPM, and the supernatant then removed, so that 2 ml of the lower layer remained. Eight ml of the saturated NaCl solution was added and centrifuged again for 5 min at 1500 RPM. A standard quantity of the surface layer was then taken from the centre, where the oocysts concentrate, placed on slides, and immediately examined under 100× magnification to determine the presence and the number of oocysts. The whole slide was examined to avoid errors arising from oocyst clustering. The intensity of *Isospora* infection was estimated as the number of oocysts per faecal drop (OPD), which has been shown to be a reliable method (Dolnik 2006). Parasite species were identified under high magnification (1000×).

To relate the prevalence and intensity of *Isospora* infection of host species to feeding behaviour, bird species were grouped according to their feeding stratum, gregariousness, and diet (Glutz von Blotzheim & Bauer 1985–1997). Foraging strata were categorised into: (1) aerial feeders: birds that catch insects in the air, (2) 'gleaners': birds that collect food from vegetation above ground, and (3) ground-foraging birds. Foraging behaviour was grouped according to the hosts' gregariousness (McQuistion 2000, modified): (1) 'single': solitary forager, (2) 'pair': birds foraging in pairs, and (3) 'flock': foraging in flocks. Species were clustered into three groups according to diet: (1) insectivores, (2) insectivores that also eat fruit, mainly during migration, and (3) seed eaters. The average intensity of infection was calculated for infected birds only. Data are presented as means ± SE.

We applied Generalized Linear Models (GLM) to analyse the effects of the hosts' foraging behaviour on their Coccidia infection. We used a Poisson error distribution with a logit link function (McCullagh & Nelder 1989) to model the influence of diet, foraging stratum and gregariousness on prevalence and intensity (cubic root transformed) of infection.

Table 1. *Isospora* spp. infection in juvenile passerine birds on the Courish Spit. For each species the number of birds infected, sample size, and infection intensity (oocysts per faecal drop, OPD) are given. Bird species were grouped by foraging parameters. *Foraging stratum*: 1 = aerial feeders, 2 = gleaners of above-ground vegetation, 3 = ground feeders. *Gregariousness* (Greg): 1 = single feeders, 2 = feeding in pairs, 3 = foraging in flocks. *Diet*: 1 = insectivores, 2 = insectivores that include fruits into diet, 3 = granivores.

Bird species	*n* infected / *n* sampled	Infection intensity (OPD)	Stratum	Greg	Diet
Acrocephalus palustris	6/14	123	2	1	1
Acrocephalus schoenobaenus	8/10	463	2	1	1
Acrocephalus scirpaceus	27/51	38	2	1	1
Aegithalos caudatus	4/7	13	2	3	1
Carpodacus erythrinus	49/72	3457	2	2	3
Certhia familiaris	1/3	50	2	1	1
Coccothraustes coccothraustes	4/4	855	2	2	3
Cyanistes caeruleus	5/20	9	2	3	2
Delichon urbica	0/3	-	1	1	1
Emberiza schoeniclus	3/5	30	2	1	3
Erithacus rubecula	19/31	2941	3	1	2
Fringilla coelebs	61/69	1131	3	2	2
Ficedula hypoleuca	2/5	7	1	1	1
Hippolais icterina	3/8	167	2	1	1
Hirundo rustica	1/2	1	1	1	1
Luscinia luscinia	8/10	374	3	1	1
Motacilla alba	17/18	457	3	2	1
Muscicapa parva	0/2	-	1	1	1
Muscicapa striata	0/6	-	1	1	1
Parus major	8/12	92	3	2	2
Passer domesticus	3/3	346	3	3	3
Phoenicurus phoenicurus	2/6	6	2	1	1
Phylloscopus colybita	5/8	370	2	1	1
Phylloscopus trochilus	38/54	1150	2	1	1
Prunella modularis	2/3	26	2	1	1
Pyrrula pyrrula	3/5	672	2	3	3
Regulus regulus	21/24	16	2	3	1
Remiz pendulinus	2/19	2	2	3	1
Spinus spinus	5/9	2276	2	3	3
Sturnus vulgaris	51/61	9472	3	3	2
Sylvia atricapilla	39/52	386	2	1	2
Sylvia borin	53/66	403	2	1	2
Sylvia communis	15/25	21	2	1	2
Sylvia curruca	16/23	130	2	1	2
Troglodytes troglodytes	2/4	185	3	1	2
Turdus merula	2/4	70	3	3	2
Turdus philomelos	0/3	-	2	3	2
Total: 37 species	**480/721**				

A priori, we defined several biologically meaningful hypotheses which we compared for each response variable (prevalence and intensity) separately. Prevalence and intensity of infection may solely depend on foraging strata (str), gregariousness (gre), or diet (die) alone. Furthermore, we examined whether prevalence and intensity may be best explained by models which additively combine the main effects of two or three of these factors (e.g. str + gre, gre + diet or str + gre + die). Some models also contained interactions between factors. However, we only considered 2-way interactions that were biologically meaningful, for example between gregariousness and diet (gre × die).

To select the best model from our candidate model set we used Akaike's information criterion (AIC; see Burnham & Anderson 2002). We calculated the Akaike's weight for each model, which can be interpreted as the probability that the current model is the best one. The best model according to AIC is the model which at the same time receives most support from the data, and uses least number of explaining factors. All the statistical analyses were performed with the R 2.7.2. Programme (R Development Core Team 2007).

RESULTS

More than 99% of the oocysts found belonged to the genus *Isospora*. A few cases of mixed infection, including *Caryospora* spp. or *Eimeria* spp., were recorded, but with low numbers of oocysts. These mixed infections were excluded from the analysis. Of the 721 birds examined, 480 (66.6%) were infected with *Isospora* spp. (Table 1). The average intensity of infection was 1870 ± 21 OPD. No oocysts were found in House Martin *Delichon urbica*, Redbreasted Flycatcher *Muscicapa parva*, Spotted Flycatcher *M. striata* and Song Thrush *Turdus philomelos*. Not taking into account the species of which less than five birds were sampled, the highest average prevalence with *Isospora* spp. (94%) was found in White Wagtail *Motacilla alba*. The largest average intensity of infection was found in Common Starling *Sturnus vulgaris* (9472 ± 490 OPD). Comparing species, prevalence of infection was positively correlated with infection intensity (Spearman rank correlation: r_s = 0.60, n = 33, $P < 0.001$).

Prevalence of infection and infection intensity depended on the stratum, the gregariousness and the diet of the hosts, and on the interaction between stratum and gregariousness (Table 2 and 3). Gleaners foraging in flocks were not only less likely to be infected but also carried lower intensities of infections than gleaners

Table 2. Prevalence of *Isospora* spp. infection of birds with respect to their foraging habits. Results of model selection for the five highest ranking models (sorted by AIC-values, with model weight).

Predictors[a]	No. of parameters	AIC	ΔAIC	Weight w_i
str+gre+die+str×gre	5	864.34	0	0.749
str+gre+die+str×die	5	867.82	3.48	0.132
str+gre+die	4	868.82	4.48	0.080
str+gre+die+sie×gre	5	870.39	6.05	0.036
str+gre	3	876.09	11.75	0.002

[a]The response variable was *Isospora* spp. occurrence (presence/absence). Predictor variables were foraging strata (str), gregariousness (gre) and diet (die) of the birds.

Table 3. Intensity of *Isospora* spp. infection of birds with respect to their foraging habits. Results of model selection for the three highest ranking models (sorted by AIC-values, with model weight).

Predictors[a]	No. of parameters	AIC	ΔAIC	Weight w_i
str+gre+die+str×gre	5	1859.16	0	0.998
str+gre+die	4	1873.98	14.82	0.001
str+gre+die+sie×gre	5	1874.10	14.94	0.001

[a]The response variable was *Isospora* spp. intensity (number of oocysts per faecal drop, OPD). Predictor variables were foraging strata (str), gregariousness (gre) and diet (die) of the birds.

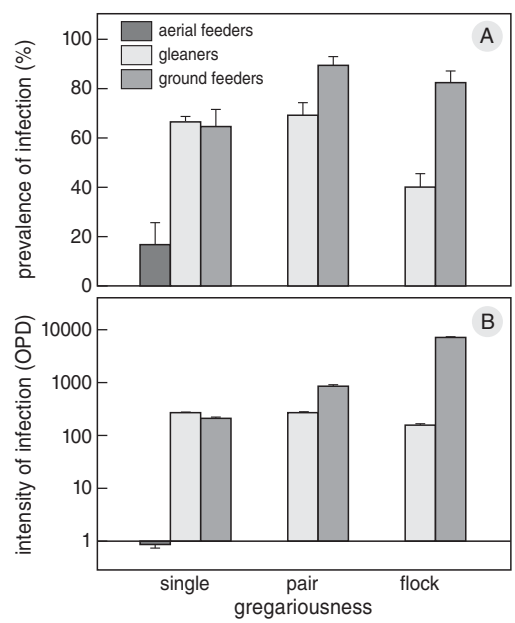

Figure 1. Prevalence (A) and intensity (B) of *Isopora* spp. infection in passerine birds grouped by gregariousness and foraging strata.

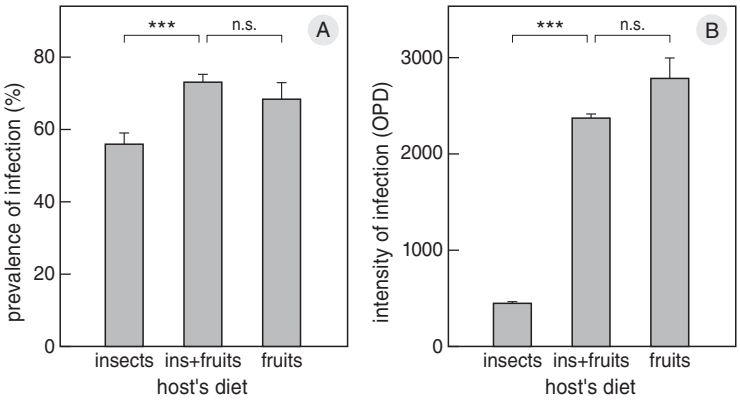

Figure 2. Prevalence (A) and intensity (B) of *Isospora* spp. infection in passerine birds grouped by main diet.

foraging alone or in pairs (Fig. 1A and 1B). Within flock feeders, gleaners were less often infected and carried lower oocyst intensities than ground foragers. The difference in prevalence and intensity between gleaners and ground foragers was smaller for species foraging in pairs and absent for species foraging alone. Both the prevalence and the intensity of infection were lowest in strict insectivores (Fig. 2).

DISCUSSION

The observed overall prevalence of *Isospora* parasites in birds in this study (66.6%) was considerably higher than that previously recorded in other published samples: 38% for birds in Germany (Scholtyseck 1956), 36.8% for birds in Czech Republic (Svobodová 1994), and 20.9% in South American birds (McQuistion 2000). There are at least two reasons why this study found a higher prevalence. First, since the production of oocysts varies with time of day with a peak production in the late afternoon (Boughton 1933, Schwalbach 1960, Dolnik 1999a,b) then birds caught earlier in the day would be identified as not infected. The previous studies trapped birds in the morning when observed prevalence would have been lower, whereas we only considered samples collected in the late afternoon. Secondly, infection intensity is lower in adult than juvenile birds (Dolnik 2002) and this is often so low that it approaches the limit of detection which would bias the results towards lower prevalence. We avoided this issue in this study by selectively sampling only juveniles.

To interpret the differences in prevalence and intensity of infection between different bird species, we need to understand the processes that shape the likelihood of infection. Each new (incident) case enters a prevalence pool and remains there until the individual either recovers or dies (Coggon *et al.* 2003). *Isospora* spp. of wild passerine birds are low-virulent parasites (Mazgaisky & Kędra 1998, Dolnik 2002, Zinke *et al.* 2003), but the recovery rate is also low (e.g. Milde 1979, Dolnik 2002, Gallazzi *et al.* 2003, Hõrak *et al.* 2004). This leads to a long period of infectiousness when even a low incidence will produce a high prevalence, because *prevalence = incidence × average period of infectiousness* (Coggon *et al.* 2003). Consequently, we propose that in case of *Isospora* spp. infection of passerine birds, the prevalence of infection reflects primarily the probability of the bird's exposure to oocysts. Even though the ingestion of infectious oocysts by the host usually results in infection (e.g. Long 1982, Dolnik 2002, Hõrak *et al.* 2004), the intensity of infection that develops within the bird can vary tremendously (Dolnik 2006). There are at least three factors that are important in increasing the intensity of coccidia infection in wild birds: (1) The frequency of re-infection (Dolnik 2002); (2) infection with a high dose of sporulated oocysts, which can lead to higher chronic infection level for a longer period (Dolnik 2002); and (3) the presence of concomitant infections, which can weaken the host and increase the severity of infection (e. g. Long 1982, Valkiūnas 2004). All three of these factors depend on exposure of the host to the faeces containing infective oocysts, which in its turn is dependent on the birds' foraging and feeding habits.

By revealing a relationship between both prevalence and intensity of infection and also the relationship between foraging parameters and infection our results support the hypothesis that *isospora*n infection in wild passerine birds depends on host foraging and feeding habits. Although these findings are essentially correlational, our analysis reveals some of the processes that could generate these associations.

Effects of stratum. Aerial feeders had the lowest prevalence and intensity of infection, and ground feeders the highest and we assume this corresponds to exposure of birds to infective oocysts in each of the strata. Avian *Isospora* oocysts are excreted with bird faeces and contaminate the ground, leaves, branches, and fruits but are also very sensitive to direct sunlight and desiccation (Martinaud *et al.* 2008). We expect therefore that shady humid ground would provide the optimal habitat where infectious oocysts would accumulate, survive, and also be available for ingestion by hosts. Consequently, ground feeders are more exposed to infective oocysts than birds feeding above ground in trees and bushes, and the least exposed are the aerial feeders and this may explain the differences in prevalence of *Isospora* infection between these bird groups (Fig. 1). Frequent exposure of ground feeders to contaminated faeces can also lead to a greater intensity of infection, due to repeated re-infections and may also be a result of coinfection with other parasites.

Interestingly, none of the heavily infected ground feeders showed signs of severe parasitemia and so it might be the case that as a consequence of continued exposure, ground feeders are more tolerant to coccidian infection than birds that forage in other microhabitats. Nevertheless, even juvenile aerial feeders showed some infections with *Isospora* Coccidia. Potentially, these juveniles might have been directly infected by their parents in the nest, as suggested by Svobodová & Cibulková (1995) and Dolnik & Loonen (2007) while infection of adult aerial feeders may have occurred during bathing, collecting nest material, or pairing.

Effects of gregariousness. Foraging in flocks may cause an aggregation of faeces at feeding sites, and therefore we can expect social foragers to be more exposed to coccidian infection. Indeed, in poultry, coccidiosis is known to spread rapidly within a group (Long 1982). This is probably because in the poultry industry, many individuals are kept at high densities within the confines of a single location and this increases the risk of rapid exposure and spread of infection. In contrast, wild birds range widely and stay at a particular site only for a short period of time. Thus, although flocking birds are indeed exposed to high amount of faeces, these are fresh and contain recently excreted unsporulated oocysts. Such oocysts usually do not cause infection (Long 1982).Our results contrast with the data of McQuistion (2000), who demonstrated for South American birds a higher prevalence of coccidian infection in gregarious species compared to single foragers. However, his data might not be in conflict with the present study, if the studied species have been biased towards ground feeders or to one particular diet group. Unfortunately, the publication did not supply a list of investigated species, which makes it impossible to explore this hypothesis further.

Although direct host-to-host transmission of *Isospora* spp within a flock is likely to be low, flocks facilitate the transmission of many other parasites such as ectoparasites and viruses, which could compromise the avian immune system and lead to higher intensities of coccidia. Higher infection intensity of gregarious birds might arise with a high primary dose of oocysts which could happen at the foraging places of flock foragers. For infection, excreted oocysts need time for sporulation so we suggest that in single and partly in pair foragers, the probability of ingestion of contaminated food would play the major role in transmission, whereas in flock foraging birds the sporulation time and survival rate of oocysts in the environment would play the main role. Thus, in gregarious birds, the exposure to live sporulated oocysts will depend not only on the foraging strata, but also on the frequency of feeding habitat use. This frequency, in its turn, often depends on what kind of food is collected, on the diet of the birds.

Effects of diet. Insects are less likely to be contaminated with sporulated oocysts than berries or seeds, which would result in both a lower probability of exposure and a lower dose for insectivores in comparison with birds that include berries into diet and granivores. The higher component of protein in the diet of insectivores can also play a role in the susceptibility and so severity of coccidia infection (Sharma *et al.* 1975). In contrast, birds that include fruits into diet are more likely to be exposed, because trees and bushes with ripe fruits attract many birds which result in accumulation of faeces and subsequent transmission. As such we expect these birds will be more often and more intensively infected with *Isospora*. Interestingly, our results show lower *Isospora* spp. prevalence in insectivores than the data of McQuistion (2000), who recorded in South American passerine birds, insectivores had a significantly higher prevalence of *isospora*n infection than frugivores. This discrepancy can be partly due to differences in other habits of the bird species, like gregariousness or foraging strata, as well as strong differences in fruit components and diet composition between South American fruit eaters and European birds that include berries in their diet. The latter suggestion is indirectly supported by the observation that the prevalence of infection is similar to the one described for European birds (Zinke *et al.* 2003, Lopez *et al.* 2007).

Combined effects. The results of model selection revealed that the prevalence and intensity of *Isospora* infection in wild passerine birds depended on all three factors: hosts foraging strata, gregariousness and diet and the interactions between foraging strata and gregariousness (Table 2, 3). A closer look at these interactions revealed some interesting details (Fig. 1). For example, in pair foragers and flock feeders, the prevalence and especially the intensity of infection increased from gleaners to ground feeders. In contrast, in single foragers, both prevalence and intensity of infection were similar between gleaners and ground foragers, probably due to the fact that exposure to the faeces of the same bird species for single foragers is similar in both strata. It is interesting to note that gleaners foraging in trees and bushes in flocks were less often and less intensively infected than gleaners foraging alone or in pairs. This could be partly a consequence that when birds are foraging alone or in pairs, they can return to the same feeding location and ingest sporulated oocysts. If this feeding location was visited by a flock of birds, it might not contain enough attractive food for the next flock of the same bird species at the next day.

Within flock feeders, gleaners foraging in trees and bushes had much lower prevalence and intensity of infection than ground foragers, but this difference was smaller in pair foragers and hardly existed in single foragers (Fig. 1), supporting the hypothesis that the main factors influencing infection transmission differ between single and flock foragers (see above).

Our study showed that even insectivorous ground feeders may face a high probability of infection with *Isospora* spp., which is illustrated by the highest prevalence of infection found in White Wagtails. The highest intensity of infection, however, was found in The Common Starling, an omnivorous bird that often forages in flocks on the ground, illustrating the foraging habits that would most affect infection intensity.

Finally it is worth noting that prevalence of infection in bird species was positively correlated with their infection intensity. Because avian *Isospora* are host-specific (e.g. Schrenzel *et al.* 2005), we would expect that parasite species with low prevalence would compensate for this by increasing the probability of successful transmission through higher oocysts production. However, bird species with low prevalence of infection were mostly aerial feeders, single foragers or insectivores. In these host groups, a continuous and high production of oocysts would hardly increase the probability of transmission to a new host. We propose that parasites in which the likelihood of exposure to infective oocysts is rare would evolve alternative mechanisms to maximize transmission success such as the vertical transmission from parents to offspring, and this type of vertical transmission should also lead to reduced virulence. If this were the case then the low level of oocysts output in juvenile aerial feeders is irrelevant for the primary route of transmission. Future investigation on this topic may reveal more information on host–parasite interactions.

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SAMENVATTING

Coccidiën zijn eencellige parasieten waar veel zangvogels in het wild mee te maken hebben. Er bestaan echter grote verschillen tussen vogelsoorten in het voorkomen van deze parasiet en de intensiteit van de infectie. De uitwerpselen van geïnfecteerde vogels bevatten oöcysten die een bron van een nieuwe infectie kunnen vormen wanneer een andere vogel ze binnenkrijgt. De verwachting is daarom dat de parasieten van de een op de andere vogel worden overgedragen tijdens het vergaren van voedsel. En dat de mate waarin een soort blootgesteld is aan infecties, afhangt van de manier waarop deze voedsel zoekt. In dit onderzoek werd daarom gekeken naar het verband tussen het voorkomen en de mate van infectie van coccidiën bij wilde vogels en hun wijze van voedsel zoeken: waar zoeken ze voedsel (in de lucht, in begroeiing, op de grond), doen ze dat alleen of in groepen en waar bestaat hun voedsel uit (insecten, insecten en vruchten, zaden). Op grond van 721 uitwerpselen van 37 vogelsoorten werden duidelijke verschillen in de mate van infectie gevonden tussen de soorten. Ten delen waren die verschillen te herleiden tot verschillen in de wijze waarop de soorten voedsel zoeken. De sterkste besmetting kwam voor bij soorten die op de grond voedsel zoeken (zoals de Spreeuw *Sturnus vulgaris*). De geringste infectie werd aangetroffen bij insecteneters. Huiszwaluw *Delichon urbica* en vliegenvangers waren bijvoorbeeld vrij van coccidiën. (BIT)

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