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Afro-Palaearctic migrant birds rid themselves of haemoparasite infections when breeding in the temperate zone

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In migratory passerines, the prevalence and parasitaemia of blood parasites often increase towards the end of the breeding season. Consequently, post-breeding migration to winter quarters can be seen as a strategy to avoid the rising pathogen pressure during this time (migratory escape). I studied haemoparasite infections in sedge warblers (*Acrocephalus schoenobaenus*) inhabiting natural wetlands in southern Poland, examining the same individuals just after their arrival from wintering grounds, and again during incubation or nestling feeding. The birds were found to be infected more often immediately after arrival than during subsequent sampling. Parasitaemia also decreased significantly as the season progressed. The health status of individuals appeared to improve during the breeding season, whereas the higher level of parasitaemia just after arrival suggests that infections had occurred earlier, on the wintering grounds or during migratory stopovers.

Bird migrations are among the most spectacular natural phenomena. Although aspects of the origin and evolution of migration are still topics of lively debate (e.g.[1–3]), the most widely accepted cause of bird migration is the seasonality in climate and resource availability[4,5]. Avoiding harsh winters must be favoured by natural selection. However, given the high costs of migration[4,6], it is less evident why birds return to the north. Commonly invoked advantages involve reduced competition[7] and predation[8] as well as excess resources at higher latitudes[5,9]. Recently, Winger et al.[3] indicated the selective benefits of breeding-site fidelity as the ultimate factor driving birds to undertake the return journey to their breeding sites.

A complementary explanation of migration could involve the high pressure of pathogens (such as viruses, bacteria or protozoans) in the areas of their transmission as a factor that may promote migration[10,11]. In support of this concept, a phylogenetic reconstruction of the evolutionary history of Afro-Palaearctic passerines has shown that northward migration evolved three times more frequently in Africa-resident species (i.e. from pathogen-rich areas) than southward migration in Palearctic-resident species (i.e. from low-pathogen areas[2]). Migrants leaving the pathogen transmission area reduce the risk of becoming infected (migratory escape[12]). The consequence of migration may also be a reduced pathogen prevalence in the population due to the higher mortality rate among infected migrants (migratory culling[13]), which could become apparent in a species' demography[14]. Studies of migratory songbirds often demonstrate that the prevalence and intensity of haematozoan infections are lowest in their winter quarters, increase during the migration period and peak during breeding[15–19].

The mortality of infected birds, however, raises the question of immune defence costs[20], because migration-related demands[6,21] may deplete resources available for mounting an immune response before and during migration[22–24]. In light of the dependence of immune investments on resource availability, I hypothesize that the breeding grounds as the target habitat for birds, despite the migration and breeding effort, enable returning birds to recover sufficiently to rid themselves of vector-borne haemoparasites acquired outside the breeding season. This might be one of the complementary factors promoting selection to return to the north. The presence of pathogens in birds returning to their breeding grounds would, on the one hand, confirm that pathogens can be transferred over long distances[25,26]. On the other, however, assuming the gradual recovery of individuals on their breeding grounds, the potential for disease transmission to other birds would be restricted to only a short period after arrival in spring, determined at the same time by the co-occurrence of competent vectors. Migrating to the northern hemisphere in spring may not only be a way to escape pathogens, but also to visit a favourite healing habitat.

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Methods

Study area

Blood samples were collected from sedge warblers (*Acrocephalus schoenobaenus*) during 2002–2007, 2016–2017 and 2019 in natural wetlands situated between two anastomosing side arms of the River Nida in southern Poland (20°28′–20°32′ E, 50°33′–50°35′ N). The two study plots (36 ha and 13.5 ha) were overgrown with patches of tall wetland vegetation, mainly common reed (*Phragmites australis*), cattail (*Typha latifolia*) and sweetgrass (*Glyceria maxima*), surrounded by extensive sedge areas (*Carex* spp.) and meadows in drier places (see[27] for a detailed description of the study area).

Study species

The sedge warbler is a small, insectivorous, long-distance migrant passerine that inhabits wetlands throughout most of Europe (except for much of the Mediterranean) and overwinters in sub-Saharan Africa. Most birds return in spring to their European breeding sites from early April to mid-May and depart between mid-July and mid-August[28]. Sedge warblers most likely first encounter and become infected with haemosporidians during overwintering[25,26]. The prevalence of avian malaria parasites (*Haemoproteus* and *Plasmodium*), previously estimated in the studied population by nested PCR, was 61%, and among the parasites detected, the SW1 and SW3 lineages of *Haemoproteus belopolskyi* were the most prevalent, accounting for 93% of all infections[29]. Long-term studies of this population revealed that males usually arrived from their wintering grounds in late April and early May, with females arriving on average 1–2 weeks after the males[30,31]. The vast majority of birds used in the current study arrived between 20 April and 20 May (93% of the total; 97% of the males).

Field procedures

Throughout each breeding season, detailed surveys of the whole study area were carried out three times a week. As a rule, males were mist-netted immediately on arrival (i.e. when first spotted), whereas females, owing to the more secretive nature of their behaviour, were often first recorded and caught only during the mating and incubation periods. The captured birds were ringed with a numbered aluminium ring and a unique combination of three coloured plastic rings, enabling subsequent identification in the field. To reflect individual body size, tarsus length was measured to the nearest 0.1 mm. A blood sample (10–30 µl) was obtained by brachial vein puncture from each bird and used to prepare two thin smears, which were air-dried at once, then fixed in the lab in 95% methanol and stained with Hemacolor (Merck). The procedure was repeated when the marked birds were recaptured later, during the late incubation or feeding periods. Across all the study years, a total of 98 males and 19 females were captured and blood-sampled twice within the same season. No individuals in this dataset were double-inspected for parasites in more than one year. Recapturing took place 4–96 days after the first capture (mean = 31 days, mode = 14 days, SE = 1.57; range of dates: 28 April–11 August; Fig. 1).

Determination of haemoparasite infections

After each breeding season the microscope slides were examined for the presence of haemosporidians (genera: *Plasmodium*, *Haemoproteus*, *Leucocytozoon*) and haemogregarines (genus *Lankesterella*; a previous study in this population revealed that the observed putative *Hepatozoon* spp. parasites were most likely *Lankesterella*[32], a finding recently confirmed by Chagas et al.[33]). The detected parasites were assigned to the relevant genus. For

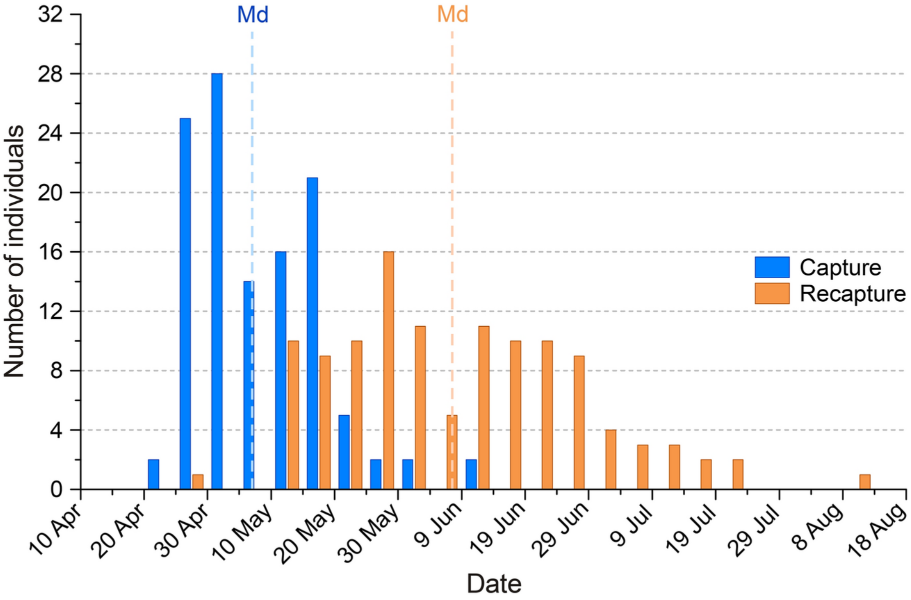

Figure 1. The distribution of capture and recapture dates of sedge warblers analysed for haemoparasite infections in the River Nida wetlands, southern Poland. Md—median.

each slide, 100 fields at 1 600 x (Nikon 50i light microscope) were checked by the same person (W.B.) and parasites of each genus were counted.

Data processing and statistical analysis

Prevalence was defined as the percentage of infected birds in a sample of birds. For each individual, the level of parasitaemia (i.e. infection intensity) of each parasite type was expressed as the number of parasites per sample (i.e. 100 microscopic fields). Instead of using the full notation (e.g. '728 parasites/100 fields'), a simplified version ('728') was used when reporting results. Total parasitaemia refers to the sum of all parasites from all genera found in the sample (100 fields). Based on the counted level of total parasitaemia, each bird was assigned to one of the following arbitrary parasitaemia categories: uninfected (0), low (≤ 20), moderate (21–100) and high (> 100). This categorization illustrates how the distribution of birds with different parasitaemia levels changes over the season.

Traditional microscopy can underestimate the true blood parasite prevalence and parasitaemia when compared with more sensitive molecular methods[29,34]. On the other hand, neither microscopy nor PCR-based methods are capable of detecting low-level or latent infections[35]. Despite the possibility of some mild infections being overlooked in a few presumably chronically infected birds, the level of error in parasite detectability should generally be the same for samples from both the first capture and the recapture. To test this, smears from 10 randomly selected infected individuals were scanned twice. The repeatability of parasite counts, calculated as intraclass correlation coefficient from one-way ANOVA[36] was very high ($R = 0.99$, $F_{9,10} = 136.3$, $p < 0.0001$). Therefore, microscopic examination of blood smears can be considered sufficient to detect and quantify within-individual changes in parasitaemia over the course of a season.

Accurate age determination is not possible in adult sedge warblers[37,38]. However, as most local recruits were first detected in the study population in their second year of life[14], it was assumed that the new arrivals were dominated by second-year individuals. Accordingly, adult birds were placed in the following age classes: 2—all first-time trapped, unringed birds, along with local recruits in their second calendar year (i.e. in their first breeding season), 3, 4 and so on—birds returning to the study area in their second or subsequent breeding seasons. The date of the first observation of a male guarding a female was considered to be his mating date. This behaviour is easy to observe in sedge warblers and usually coincides with the cessation of male song[39]. To make arrival and mating dates comparable between seasons, each date was coded the same way each year, i.e. 1 April was made equal to 1, and subsequent dates were coded in ascending order. To determine the quality of a male's territory, circular spatial buffers 30 m in radius were delimited on a digital vegetation map in ArcGIS ver. 10.1 around all the song-posts of each male on the day of his arrival. Territory quality was then defined as the average proportion of preferred tall wetland vegetation cover (cattail and common reed) in the buffers of a given male (see[27,40] for details).

Changes in infection prevalence and the distribution of individuals with different levels of parasitaemia between the first-capture and the recapture samples were analysed using Chi-square test. Since the transformed parasitaemia values did not meet the criteria for normality and homogeneity of variance, non-parametric tests and generalized linear models (GLM) with non-transformed data were used for all subsequent analyses. Parasitaemia levels in the first and second samplings of the same birds were compared using the paired-samples sign test. Due to within-individual changes in status (gain or loss) and components of a mixed infection during the season, the paired test was not performed for mixed infections. Analyses of the relationship between parasitaemia, arrival date and other variables were restricted to males only, as the sample of females was small and, moreover, the first-capture dates of females did not adequately reflect their arrival dates. The change in total parasitaemia levels between the first capture and recapture of males was analysed as a response variable using GLM multivariate analysis of repeated measures in relation to year, age, arrival date, territory quality, tarsus length, and breeding success (in terms of the number of fledglings reared during the breeding season) as predictors. The effects of initial parasitaemia on male mating date, mating success (binomial: 1—success, 0—no success) and breeding success (binomial: 1—success in rearing at least one fledgling during the season, 0—no success) as response variables were analysed using GLM, with arrival date and year as covariates in all models. The Akaike information criterion (AIC) was used to select the best-fitting model with the appropriate distribution and link function. QPweb ver. 1.0.15[41] was applied to calculate 95% confidence intervals (CIs) of prevalence, using Sterne's method[42,43], and 95% CIs of mean parasitaemia, using bias-corrected and accelerated bootstrap CI[44]. All other statistical analyses were performed using SPSS v.23 (IBM SPSS Statistics) and Statistica 13.1 (Dell Inc.). The level of significance in all the analyses was set at $p < 0.05$.

Ethics approval

The research reported here complied with all the legal ethical requirements and legislation of Poland. Field procedures were carried out under the permits from the Local Ethical Committee in Kraków (nos. 37/OP/2004, 143/2015 and 217/2019) and were reported in accordance with the ARRIVE guidelines.

Results

General data on haemoparasites

Overall, three haematozoan genera were detected in the sample of double-inspected sedge warblers: *Haemoproteus*, *Lankesterella* and *Plasmodium*. *Haemoproteus* infections were the most prevalent (Table 1) and the majority of infected individuals carried only the gametocytes of this genus (first capture: 65% of males and 81% of females; recapture: 47% of males and 70% of females). Mixed infections with parasites from two or three genera occurred in one-fifth of males but in only two females in both the first-capture and the recapture samples (Table 1). No *Plasmodium* infection was found in any of the females from the first capture.

Infection type	Sample	Prevalence				Parasitaemia (infected)		Change in parasitaemia (all)	
		First capture	Recapture	χ^2	p	First capture	Recapture	Z	p
Haemoproteus	Males	72.4 (62.8–80.7) 71	42.9 (33.1–53.1) 42	17.6	< 0.0001*	39.9 (23.0–78.5) 1–728	8.5 (5.1–15.0) 1–78	6.4	< 0.0001*
	Females	78.9 (55.4–92.5) 15	47.4 (25.7–68.8) 9	2.8^{Y}	0.093	98.8 (31.6–34.7) 1–916	6.2 (3.1–12.6) 1–22	2.4	0.016*
	All	73.5 (64.6–80.9) 86	43.6 (34.6–53.0) 51	21.6	< 0.0001*	50.2 (29.9–95.1) 1–916	8.1 (5.2–13.7) 1–78	6.9	< 0.0001*
Lankesterella	Males	19.4 (12.6–28.5) 19	18.4 (11.6–27.5) 18	0.03	0.855	1.8 (1.3–3.4) 1–9	1.8 (1.4–2.3) 1–4	− 0.0	1.0
	Females	15.8 (4.4–39.2) 3	10.5 (1.9–31.6) 2	0.0^{Y}	1.0	1.3 (1.0–1.7) 1–2	5.0 (2.0–5.0) 2–8	− 0.5	0.617
	All	18.8 (12.6–26.9) 22	17.1 (11.0–25.1) 20	0.1	0.733	1.8 (1.3–3.1) 1–9	2.2 (1.6–3.2) 1–8	0.0	1.0
Plasmodium	Males	10.2 (5.4–17.7) 10	13.3 (7.4–21.3) 13	0.4	0.506	2.4 (1.3–5.1) 1–10	2.2 (1.6–2.8) 1–4	0.8	0.453
	Females	0.0 0	5.3 (0.3–25.7) 1	0.0^{Y}	1.0	– –	2.0 (–) 2–2	–	–
	All	8.5 (4.6–15.3) 10	12.0 (7.1–19.1) 14	0.7	0.389	2.4 (1.3–5.2) 1–10	2.4 (1.3–5.2) 1–4	1.0	0.332
Mixed infection	Males	20.4 (13.2–29.5) 20	19.4 (12.6–28.5) 19	0.03	0.858	32.7 (13.0–101.0) 2–360	13.9 (7.5–28.5) 2–79	–	–
	Females	10.5 (1.9–31.6) 2	10.5 (1.9–31.6) 2	0.3^{Y}	0.597	73.0 (10.0–136.0) 10–136	11.5 (5.0–11.5) 5–18	–	–
	All	18.8 (12.6–26.9) 22	17.9 (11.8–26.0) 21	0.03	0.866	36.4 (16.0–91.5) 2–360	13.7 (7.6–28.0) 2–79	–	–
Total infection	Males (98)	79.6 (70.5–86.8) 78	54.1 (43.9–63.8) 53	14.4	0.0001*	37.1 (21.6–76.4) 1–728	7.9 (5.1–13.6) 1–79	5.6	< 0.0001*
	Females (19)	84.2 (60.8–95.6) 16	52.6 (31.2–74.3) 10	3.0^{Y}	0.081	92.9 (29.2–319.0) 1–916	6.8 (3.3–12.7) 1–22	2.1	0.039*
	All (117)	80.3 (71.9–86.9) 94	53.8 (44.4–62.9) 63	18.6	< 0.0001*	46.6 (28.2–84.8) 1–916	7.7 (5.3–12.7) 1–79	6.1	< 0.0001*

Table 1. Prevalence and parasitaemia of haemoparasite infections in repeatedly measured sedge warblers from the River Nida wetlands. For prevalence, the 95% CIs (in brackets) and the number of infected birds (bottom row in each case) are given; Y—Yates correction in Chi-square tests. For parasitaemia in infected birds, the mean, 95% CIs (in brackets) and the range of parasite numbers per 100 microscopic fields (bottom row in each case) are shown. Uninfected individuals (zero levels of parasitaemia) have also been included in the paired-samples sign tests of double-inspected birds. * $p < 0.05$.

Level of parasitaemia	Males (98)		Females (19)		All (117)	
	Capture	Recapture	Capture	Recapture	Capture	Recapture
Uninfected (0)	20	45	3	9	23	54
Low (<=20)	57	49	9	9	66	58
Moderate (21–100)	16	4	3	1	19	5
High (> 100)	5	0	4	0	9	0
	$\chi^2 = 22.42$ $p < 0.0001$		$\chi^2 = 8.0$ $p = 0.046$		$\chi^2 = 30.16$ $p < 0.0001$	

Table 2. Distribution of sedge warbler males and females with different levels of total parasitaemia, presented separately for the first-capture and the recapture sample, compared by Chi-square test.

Within-season changes in parasite prevalence and parasitaemia

In the first capture of sedge warblers the range of total parasitaemia levels was extensive (0–916). Apart from 20% of uninfected individuals, 56% exhibited a low level of parasitaemia, in 16% the level was moderate, whereas in only 8% was the level very high (Table 2). There were no sex differences in total parasitaemia (Mann–Whitney U test; $Z = 1.09$, $p = 0.277$).

In the recaptured birds, both parasite prevalence and total parasitaemia were much lower than during the first capture (Table 1; Mann–Whitney U test; $Z = 5.33$, $p < 0.0001$). However, the decrease in prevalence was only significant in males, both for *Haemoproteus* infections considered separately and for total haemoparasite infections (Table 1). Among the recaptured birds, 46% were uninfected, 50% had a low level of parasitaemia and 4% exhibited a moderate level. There were no birds with total parasitaemia exceeding 79. Contingency analysis revealed a significant difference in the distribution of males and females with different levels of total parasitaemia between the first capture and the recapture (Table 2). However, there was no sex difference in either the first-capture or the recapture sample (first capture: $\chi^2 = 5.77$, $p = 0.123$; recapture: $\chi^2 = 0.08$, $p = 0.961$; Table 2). Although the prevalence of mixed infection did not change, mixed infection was significantly more likely to disappear in individuals between the two measurements (in 14/22 with mixed infection) than to appear (in 13/95 without mixed infection; $\chi^2 = 25.11$, $p < 0.0001$).

The paired comparisons test demonstrated a significant decrease in total parasitaemia between the first and second sampling of the same individuals (Table 1). A decrease in parasitaemia was also apparent in the analysis restricted to *Haemoproteus* infections (Table 1). Total parasitaemia decreased in 75 of 117 birds (64%), remained unchanged in 26 (22%) and increased in only 16 birds (14%). Five out of 23 birds (22%), found to be parasite-free at the first sampling, carried haemoparasite infections during the second sampling. Conversely, 36 out of 94 birds (38%) bearing parasites during the first sampling were found to be parasite-free in the second one. However, if we assume that a change in parasitaemia level by less than ± 5 parasites per 100 microscopic fields falls within the measurement error range (and thus go undetected; cf.[45]), then parasitaemia decreased in 44% of birds ($n = 52$), remained unchanged in 54% ($n = 63$) and increased in only 2% (two individuals – one male and one female).

Relationships between parasitaemia and individual male traits, territory quality and breeding success

In the repeated measures analysis, the change in total parasitaemia during the season was not influenced by territory quality, tarsus length, or breeding success of males, although significant effects of year, age and arrival date were observed (Table 3). Additionally, parasitaemia detected on arrival was not related to the mating status, mating date or breeding success of the analysed males (Table 4).

Discussion

The overall dynamics of parasitaemia in the studied population of sedge warblers was shaped mainly by parasites of the genus *Haemoproteus* (the most common in birds[46]). The prevalence of haemoparasite infection was high on arrival at the breeding grounds and decreased significantly later in the season (from ca. 80% to 50%); moreover, the same individuals double-inspected for parasites considerably reduced or completely rid themselves of the infection in the bloodstream during the season.

Parasitaemia was not related to the male's body size, territory quality, or breeding success. However, the significant effect of age on the change in parasitaemia during the season suggests that birds from different age cohorts may differ in their ability to recover from infection[47,48]. Nonetheless, the lack of a clear trend (no increase or decrease with age) and the very small sample size of males older than second-year in the final model ($n = 5$) prevent drawing definitive conclusions about age-related changes in parasitaemia within the season. Despite this, a decrease in infection intensity with age was previously noted in a large sample of longitudinally studied males from this population[14]. In turn, the higher parasitaemia observed in later-arriving males may indicate a link between infection and individual quality and condition, as well as the impact of infection on delayed arrival from wintering grounds[15,49–51].

The presence of severe infections in the studied population just after arrival confirms that birds can transport infectious pathogens over large distances[25,52], but is no proof of their transmission to other hosts in breeding areas (cf.[18]). A long-term study in the same population[14] demonstrated that yearling survival depends on the parasite load, which is concordant with the 'migratory culling' hypothesis[13] and confirms that a large proportion of infections are not actually transported as a result of host mortality during migration.

Studies of migratory songbirds have often demonstrated that the prevalence and intensity of haematozoan infections are the lowest in the wintering areas, increase during migration and reach a maximum during breeding[15–19]. The results presented here stand in contrast to those of previous studies. Nevertheless, this difference may be due to the research methodology applied: temporal changes in the parasite load reported within the breeding period are usually derived from a single sampling of different individuals during the season (e.g.[15,50]), and this probably demonstrates only the between-individual differences in quality and infection

Effects	df1/df2	Estimate	SE	t	F	p
Δ Parasitaemia	1, 90				263.53	< 0.0001*
Year	7, 90				37.59	< 0.0001*
Age	2, 90				1749.00	< 0.0001*
Arrival date	1, 90	0.06	0.027	2.163	4.68	0.033*
Territory quality	1, 90	0.04	0.526	0.070	0.01	0.945
Tarsus	1, 90	− 0.46	0.247	− 1.844	3.40	0.068
Success	1, 90	− 0.04	0.070	− 0.590	0.35	0.557
Δ Parasitaemia*year	7, 90				269.67	< 0.0001*
Δ Parasitaemia*age	2, 90				128.84	< 0.0001*

Table 3. Change in parasitaemia (Δ) between the first capture and the recapture of sedge warbler males (response; Poisson distribution, log-link function), analysed by GLM multivariate analysis of repeated measures, with year, age, arrival date, territory quality, tarsus length, and breeding success (number of fledglings reared) as predictors. *$p < 0.05$.

Model (n)	Response	Predictors	Estimate	SE	χ^2	p
1 (98)	Mating success	Parasitaemia	< < − 0.01	0.004	0.022	0.882
		Arrival date	− 0.04	0.028	2.144	0.143
		Year	− 0.07	0.048	2.193	0.139
2 (70)	Mating date	Parasitaemia	< < − 0.01	0.007	0.343	0.558
		Arrival date	0.46	0.106	18.397	< 0.0001*
		Year	0.14	0.108	1.709	0.191
3 (83)	Breeding success	Parasitaemia	< < 0.01	0.003	< < 0.001	0.994
		Arrival date	− 0.03	0.029	0.753	0.385
		Year	− 0.10	0.037	7.498	0.006*

Table 4. GLM models analysing the effects of parasitaemia in the first capture of sedge warbler males on their: (1) mating success (binomial variable: 1—success, 0—no success; logit link function, modelled probability that success = 1), (2) mating date (continuous variable; Gamma distribution, identity link function) and (3) breeding success (binomial variable: 1—success in rearing at least one fledgling during the season, 0—no success; logit link function, modelled probability that success = 1), as response variables. Arrival date and year (continuous variable; coded as a successive season between 2002 and 2019) were included as covariates in all models. *$p < 0.05$.

susceptibility[48,53], different phases of infection development in the bloodstream or the different origin of migration waves[54]. Conversely, sampling of the same individuals repeated within-season provides direct evidence that parasitaemia diminished in particular individuals; this measurement is straightforward. Additionally, this lower level of infection, in tandem with infection having no impact on male breeding success, has implications for the common perception of 'breeding effort', which may not be as debilitating in a species like the sedge warbler, which feeds small broods on diverse food types that remain relatively plentiful throughout the season (own unpubl. data, cf.[55]). However, it is also possible, that the relationship between parasite load and breeding success was not detected due to the small sample of males per year in the dataset, as well as the high rate of nest failure in this population caused by predation and flooding[56], which can reduce the effect of male quality on breeding success.

The stronger pressure of parasites during the breeding period is commonly explained as the reproductive cycles of different parasite taxa coinciding with those of their hosts[57,58]. Thus, the seasonal increase in parasite abundance towards the end of the breeding period is often associated with the greater availability of immunologically naive young hosts[57,59], whereas the increase may not occur intra-individually in immunocompetent adults.

The observed levels of infection can also be explained by the circannual dynamics of vector-borne diseases, which depend closely on the seasonality of vector abundance and activity, determining opportunities for parasite transmission[57,60,61]. New parasite inoculations just after the spring arrival could cause a temporary increase in infection, but they are rather unlikely in this particular host-parasite system. Firstly, in early spring there are no active *Haemoproteus* vectors in sedge warbler breeding habitats (i.e. *Culicoides* biting midges[46]). Low temperatures restrict the development, occurrence and flight activity of blood-sucking arthropods, which considerably limits the transmission of parasites to new hosts at this time[62–65]. The development of haemosporidians within their vectors is also determined by temperature[66]. Secondly, the males were mist-netted immediately after arrival, whereas it takes about two weeks from the injection of *Haemoproteus* sporozoites to the development of gametocytes circulating in the bloodstream[67,68]. Thus, the infection intensity detected in the first sample must clearly be the result of parasites having been injected before the spring arrival. Moreover, if the birds were infected just after arrival, one must expect at least some of them to have developed an acute phase by the time of recapture[46,68]. However, not a single highly parasitized individual was observed in the second trial. Thirdly, the SW1 and SW3 lineages of *H. belopolskyi*—the most prevalent blood parasites detected in this population[29]—have never been proven to be transmitted outside the wintering grounds in Africa[25,26].

In the present study, only two individuals showed a marked increase in parasitaemia during the season. Along with the absence of infections in juveniles ([69], also own unpubl. data), this confirms the lack of parasite transmission in the breeding areas. Moreover, the widespread decrease in parasitaemia, observed in most sedge warblers, may promote self-suppression of infection. If recovery of birds from infection is a common occurrence within the breeding population, then later in the season, when the abundance of *Haemoproteus* vectors is likely to increase (e.g.[64,70,71]), the probability of transmission paradoxically decreases owing to the lower proportion of bird hosts with parasites circulating in the bloodstream. The observed seasonal pattern of infection, however, is most likely the result of past coevolution between parasites, their vectors and avian hosts, which determined a specific area of parasite transmission, restricted to non-breeding areas[26].

As far as the 'migratory escape' mechanism[12] is concerned, sedge warblers, on leaving their wintering quarters and migration stopovers, probably become separated from the key factors essential for haemoparasite transmission, i.e. infected hosts and active competent vectors. Moreover, according to the complementary 'migratory recovery' mechanism[72], migrating birds can also suppress or clear acquired infections if conditions for survival, development and transmission of parasites during migration become unfavourable ([72] and references therein). While the present study demonstrates that the breeding season is the stage in the annual cycle of sedge warblers which enables them to recover from haematozoan infections, this process may well have been initiated earlier and acts in conjunction with 'migratory recovery'.

In conclusion, I have demonstrated that the haemoparasite load of the majority of repeatedly-measured sedge warblers decreased significantly between their arrival from the tropics and nest-provisioning, despite their assumed high breeding effort, which was expected to render them susceptible to infection. As migration to the temperate zone seems beneficial in this context, I suggest, in analogy with 'migratory recovery', to use the term 'breeding recovery', for migratory species, which during breeding can rid themselves of previously acquired infections.

Data availability

The datasets generated and analysed during the current study are available from the author upon request.

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Author contributions

W.B. conceived the study, collected and analysed the data and wrote the paper.

Declarations

Competing interests

The author declares no competing interests.

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