

Article

High Blood Parasite Infection Rate and Low Fitness Suggest That Forest Water Bodies Comprise Ecological Traps for Pied Flycatchers

Ronalds Krams^{1,2}, Tatjana Krama^{1,2}, Didzis Elferts³, Janīna Daukšte⁴, Patrīcija Raibarte⁴, Guntis Brūmelis³, Iluta Dauškane³, Linda Strode³ and Indrikis A. Krams^{1,4,5,6,*}

¹ Department of Biotechnology, Daugavpils University, 5401 Daugavpils, Latvia; ronalds.krams@gmail.com (R.K.); tatjana.krama@du.lv (T.K.)

² Chair of Plant Health, Estonian University of Life Sciences, 51006 Tartu, Estonia

³ Department of Botany and Ecology, Faculty of Biology, University of Latvia, 1004 Rīga, Latvia; didzis.elferts@lu.lv (D.E.); guntis.brumelis@lu.lv (G.B.); iluta.dauskane@lu.lv (I.D.); linda.strode@lu.lv (L.S.)

⁴ Institute of Food Safety, Animal Health and Environment BIOR, 1076 Rīga, Latvia; janina.daukste@inbox.lv (J.D.); patricijar9@gmail.com (P.R.)

⁵ Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia, 1004 Rīga, Latvia

⁶ Institute of Ecology and Earth Sciences, University of Tartu, 50409 Tartu, Estonia

* Correspondence: indrikis.krams@ut.ee

Simple Summary: Animals tend to settle and reproduce in high-quality habitats which provide large amounts of food and shelter against predators. Although they are attracted by abundant food resources, reproductive output and survival of animals may be affected by some other environmental factors. This study found that Pied Flycatchers (*Ficedula hypoleuca*) breeding near water bodies were caught in an ecological trap. We found that the number of fledglings, their body mass, and tarsus length were positively correlated to the distance to the lakes. The number of blood-sucking insects, adult body mass at the end of the breeding season, and the distance to the nearest water body were negatively correlated, suggesting that breeding near forest water bodies comes at a cost. More studies must be done to understand the role of different kinds of blood parasites and their vectors in fitness reduction of birds. We recommend avoiding putting bird nest boxes near forest water bodies to mitigate the damaging effects of maladaptive habitat selection of cavity-nesting birds.

Abstract: Blood parasites are considered to have strong negative effects on host fitness. Negative fitness consequences may be associated with proximity to areas where blood parasite vectors reproduce. This study tested for relationships between haemosporidian infection prevalence, parasitemia, and fitness parameters of breeding Pied Flycatchers (*Ficedula hypoleuca*) at different distances from forest water bodies. Prevalence and parasitemias (the intensity of infection) of haemosporidians and vector abundance generally decreased with increasing distance from forest lakes, streams, and bogs. Fledgling numbers were lower, and their condition was worse in the vicinity of water bodies, compared with those located one kilometer away from lakes and streams. At the beginning of the breeding season, adult body mass was not related to distance to the nearest water body, whereas at the end of the breeding season body mass was significantly lower closer to water bodies. Forest areas around water bodies may represent ecological traps for Pied Flycatchers. Installing nest boxes in the vicinity of forest water bodies creates unintended ecological traps that may have conservation implications.

Keywords: blood parasites; ecological traps; parasite vectors; Pied Flycatcher



Citation: Krams, R.; Krama, T.; Elferts, D.; Daukšte, J.; Raibarte, P.; Brūmelis, G.; Dauškane, I.; Strode, L.; Krams, I.A. High Blood Parasite Infection Rate and Low Fitness Suggest That Forest Water Bodies Comprise Ecological Traps for Pied Flycatchers. *Birds* **2022**, *3*, 221–233. <https://doi.org/10.3390/birds3020014>

Academic Editor: Jukka Jokimäki

Received: 31 December 2021

Accepted: 6 April 2022

Published: 9 April 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

The distribution of biological taxa is spatially arranged. The geographical limits to the distribution of a species are determined by abiotic factors such as precipitation and

temperature, and biotic factors involving interactions between organisms. For example, parasites can cause limitations to the distribution, habitat selection, and fitness of their host species [1,2].

Avian blood parasites can be found in numerous bird species across five continents and are transmitted by different insect vectors affecting distribution ranges, community structure, and abundance of host species. The acute phase of blood parasite infection is characterized by high parasitemia levels, which have a substantial impact on erythrocytes that cause anemia [3], affect general activity [4,5], impair growth rates and the immune system [3], and raise mortality rates of host individuals [6]. Although much lower parasitemia levels can be observed during the chronic phase of the infection, blood parasites impose substantial costs on their hosts, such as increased predation risk [7] and reduced longevity [6], reproductive performance, and overall fitness [3,6,8].

While some bird species are apparently free of blood parasites because of the efficiency of their immune systems, which detect and eliminate parasites [9], the physiological effect of blood parasites on birds largely depends on the presence and abundance of competent parasite vectors in bird habitats [3,10–12]. It has been shown that birds breeding on sea islands or by the seaside often lack blood parasites or have low blood parasite prevalence [13]. Bird blood parasites are also often lacking in the blood of birds in arid and high-altitude environments, which can be explained by the absence or scarcity of insect vectors [7,9,14–19]. Thus, the presence and persistence of vector-borne parasitic diseases are often associated with the immunity of hosts and the availability of appropriate habitats for insect vectors [7,9,20–22].

A wide range of blood-sucking insects locally transmit blood parasites. Many mosquito (*Culicidae*) species can transmit *Plasmodium* species. Mosquitoes prefer lakes, ponds, and slow rivers because they require standing water to reproduce [9,23–28]. Water-reservoir proximity is an important factor predicting higher malaria incidence in humans [29,30]. The *Haemoproteus* parasites can be transmitted by various mosquitoes, biting midges (*Culicoides*), and louse flies (*Hippoboscidae*) [31–34]. Biting midges reproduce in fens, bogs, marshes, compost, permanently wet soil, mud, and stream margins [35], whereas louse flies do not need specific abiotic conditions [31]. The *Leucocytozoon* parasites are transmitted by biting midges and blackflies (*Simuliidae*) [31]. Blackfly development requires running water such as streams. This means that insect vectors of bird blood parasites need wetlands to reproduce and develop. It also suggests that the prevalence of blood parasites may increase in birds living or breeding near wetlands. A positive association between proximity to the nearest wetlands and parasite prevalence has been shown in some forest passerine birds [24,27]. However, it is not clear whether forest stands located further away from forest lakes and streams can be considered parasite-free areas.

Previous research has shown that the prevalence of *Haemoproteus* and *Plasmodium* infections decreased with increasing distance from forest lakes and bogs in members of mixed-species groups composed of Willow Tits (*Poecile montanus*) and Crested Tits (*Lophophanes cristatus*) during the non-breeding season [7]. This study was carried out to test for associations between blood parasite prevalence, infection intensities, reproductive success, fledgling body mass, tarsus length, and the distance to the nearest forest wetland in breeding Pied Flycatchers (*Ficedula hypoleuca*). Pied Flycatchers are long-distance migrants whose blood parasites can infect birds in their wintering grounds in Africa. However, Pied Flycatchers can become infected with local blood parasites, especially because their immune system may be compromised upon a long and demanding journey from Africa to their breeding areas in northern Europe. The breeding season is also known to lower immunity [36,37].

2. Materials and Methods

2.1. Study Site and Birds

The study was conducted in the vicinity of Krāslava in southeastern Latvia (56° N, 27° E) in May and June 2018. The study area was surrounded by drainage basins of three

small forest streams that consisted of cascades of small lakes, naturally occurring ponds, beaver-constructed ponds, and bogs. This diverse system of forest water bodies provided suitable habitats for reproduction of all kinds of blood parasite vectors [7]. The study area was covered by a markedly homogeneous coniferous habitat dominated by Scots pine (*Pinus sylvestris*) monocultures with an age of about 60–70 years [38]. The high levels of homogeneity in pine stands are maintained by regular forest stand thinning and removal of young silver birch (*Betula pendula*), Norway spruce (*Picea abies*), and common aspen (*Populus tremula*) trees. In contrast, forests (c. 60–70 years-old) near water bodies contained much higher tree species biodiversity consisting of Scots pine, grey alder (*Alnus incana*), black alder (*A. glutinosa*), Norway spruce, silver birch, bird cherry (*Prunus padus*), European hazel (*Corylus avellana*), and marginally by English oak (*Quercus robur*) and common juniper (*Juniperus communis*) [38,39]. The higher tree diversity within 40–60 m zones around forest lakes, streams, and beaver constructed ponds is generally caused by mesic soil conditions and lack of forestry measures such as clear-cuts and less regular forest thinning around water bodies in the state-owned pine stands.

This population of Pied Flycatchers has been studied as part of a long-term project of the ecology of cavity-nesting birds carried out since the mid-1980s [38,40,41]. Pied Flycatcher nest boxes were mounted on pine trunks at a height of 1.5 m. We kept the entrance of all nest boxes closed until the end of April when the first migrating Pied Flycatchers arrived. This prevented the nest boxes from being occupied by Great Tits (*Parus major*), a competing cavity-nesting species. The nest boxes were arranged in lines, with adjacent nest boxes being set 95–105 m apart. We had seven lines of nest boxes, each consisting of 10 nests. However, not all nest boxes in all lines had been occupied by Pied Flycatchers. On average, birds occupied 8 nest boxes in each line. In total, the flycatchers occupied 50 nest boxes. The first nest box in a line was placed within a 20–30 m distance from a forest lake or small stream in a mixed pine/spruce/birch forest with a tall shrub layer; the most distant nest box of the line was located approximately 1 km away from the nearest water body in a pine-dominated forest with a sparse shrub layer. Nest boxes were checked to record basic breeding parameters such as clutch size, brood size, and the number of fledglings, which reflected reproductive success. No nests were depredated by pine martens (*Martes martes*) or other predators, and none were deserted due to our activities. All but two adult Pied Flycatchers were young (the first calendar-year vs. the second calendar-year and older) individuals, and, therefore, the age did not affect the results. The age of Pied Flycatchers was determined based on the shape and cover of the outer wing covert feathers [42,43].

2.2. Blood Parasites

We trapped each of the adult Pied Flycatchers twice: (1) in the first half of May when the birds started building nests, and (2) in the first half of June when their offspring reached the age of 13–15 days. Blood parasites cannot be detected in the blood until three weeks after infection [3,31], which makes the discrimination between blood parasites brought from wintering grounds and obtained in the breeding territories difficult. Therefore, we collected second blood samples of adult individuals just before the offspring fledged their nests, and did not collect the blood samples of nestlings at all. This allowed us to separate the first and second sampling events by at least a 4-week interval.

Since females almost always abandon their nests if captured in their nest boxes at the beginning of the nest building stage, we attempted to capture Pied Flycatchers in only three nest box lines (10 males and 10 females, in total). The first capture of the birds was always done by using traps designed as nest boxes which were placed 20–30 m away from the nest boxes occupied by the birds. Pied Flycatchers often inspect other cavities in their neighborhood, which made it feasible to use traps designed as nest boxes [44,45]. Importantly, these precautions and the repeated captures did not allow us to sample many adults, which is important when considering our relatively small sample sizes.

At capture, blood samples (150 μ L) were taken from the flycatcher's tarsal vein. To identify blood parasites and leucocytes, a drop of blood was smeared on two to three individually marked microscope slides, air-dried, fixed in absolute methanol, and stained with Giemsa stain [31,46]. We also took blood samples from 80 nestlings at 40 nest boxes on day 15 post-hatch to screen their blood for blood parasites. All captured and inspected individuals were marked with standard aluminum and plastic bands.

Smears were screened with a light microscope under oil immersion at 1000 \times magnification for *Haemoproteus* and *Plasmodium* and at 500 \times magnification for *Leucocytozoon* [46–48]. Parasites were enumerated from 100 fields by moving the slide to areas where blood cells formed a monolayer for *Leucocytozoon* and from more than 250 fields for *Haemoproteus* and *Plasmodium*. Slides were screened by T.K. and P.R. Individuals were classified as infected when smears were positive for at least one haemoparasite taxon. The intensity of infection (parasitemia) was estimated as the number of parasite gametocytes per 10,000 erythrocytes [31]. We also searched for all other blood parasites such as trypanosomes, haemogregarines, piroplasms, and microfilaria. These parasites, including *Leucocytozoon*, were not detected in our samples.

2.3. Estimation of Vector Numbers

To check for relationships between the number of blood-sucking insects within nest boxes and the distance to the nearest water body, we attached sticky traps to the nest boxes' ceilings. We had between 3 and 6 nest boxes occupied by Pied Flycatchers at distances of 100, 250, 400, 550, 700, 850, and 1000 m away from the nearest water body. Each trap was constructed as a square (14 \times 14 cm) of thick paper covered by a layer of non-hardening epoxide resin [3]. The trap was attached to the ceiling of the nest box using pins. We prevented adult flycatchers from sticking themselves to the sticky surface of epoxide resin by attaching a wire mesh 1 cm above the trap (mesh size 1 \times 1 cm), which did not constrain insects' movements. We removed all of the bloodsucking insects trapped daily, identified and counted them, and estimated the relative number of trapped bloodsucking insects per day.

2.4. Statistics

The effect of the distance from the nearest water body on clutch size and fledgling number was analyzed using Poisson generalized linear mixed-effects models (GLMM). Generalized additive mixed models (GAMM) were used to analyze the effect of the distance from the water body on fledgling body mass, tarsus length, and body condition. Distance from the water body, bird sex, season timing (beginning or end), and all two-way interactions between these factors were used as independent variables in the models to analyze the effects on *Haemoproteus* and *Plasmodium* prevalence (binary logistic GLMM) and parasitemia (Poisson GLMM) in adult birds. Distance from the nearest water body, season timing (beginning or end), and interaction between those factors were used as independent variables to analyze the effect on adult body mass (linear mixed-effects model, LMER). In all models, nest box line identity was used as a random factor. Additionally, bird ID was used as a nested random factor within line ID for models with *Haemoproteus*, *Plasmodium*, and adult bird body mass as there were two measurements per bird. Body condition of nestlings were estimated as residuals from the linear regression of body mass on tarsus length [49]. All models were implemented as Bayesian LMER, GAMM, or GLMM using R 4.0.2. [50] library *brms* [51]. The number of iterations was set to 3000 for each of the four chains. Rhat values (all close to \sim 1.00) were used to assess the convergence of the models. Effect or difference was considered significant if the 95% credibility interval did not contain the value 0.

3. Results

3.1. *Haemoproteus*

Haemoproteus infection prevalence did not differ between males and females, nor within each sex at the beginning of the breeding season, the end of the season, or across the

season (Figure 1A). *Haemoproteus* prevalence significantly differed only between females at the beginning of the season and males at the end of the season (difference estimate -5.55 , 95% credibility interval (CI): $(-11.71, -0.03)$; Figure 1A), suggesting a rise in *Haemoproteus* prevalence in males from the beginning to the end of the breeding season. *Haemoproteus* prevalence significantly decreased as distance from the nearest water body increased at the end of the breeding season (slope difference estimate: -4.44 , CI: $(-9.34, -1.10)$; Figure 1B) but had no significant effect at the beginning of the season (estimate -3.23 , CI: $(-7.59, 0.15)$; Figure 1B). Distance and sex interaction had no significant effect on *Haemoproteus* prevalence (estimate 3.33 , CI: $(-1.35, 8.45)$).

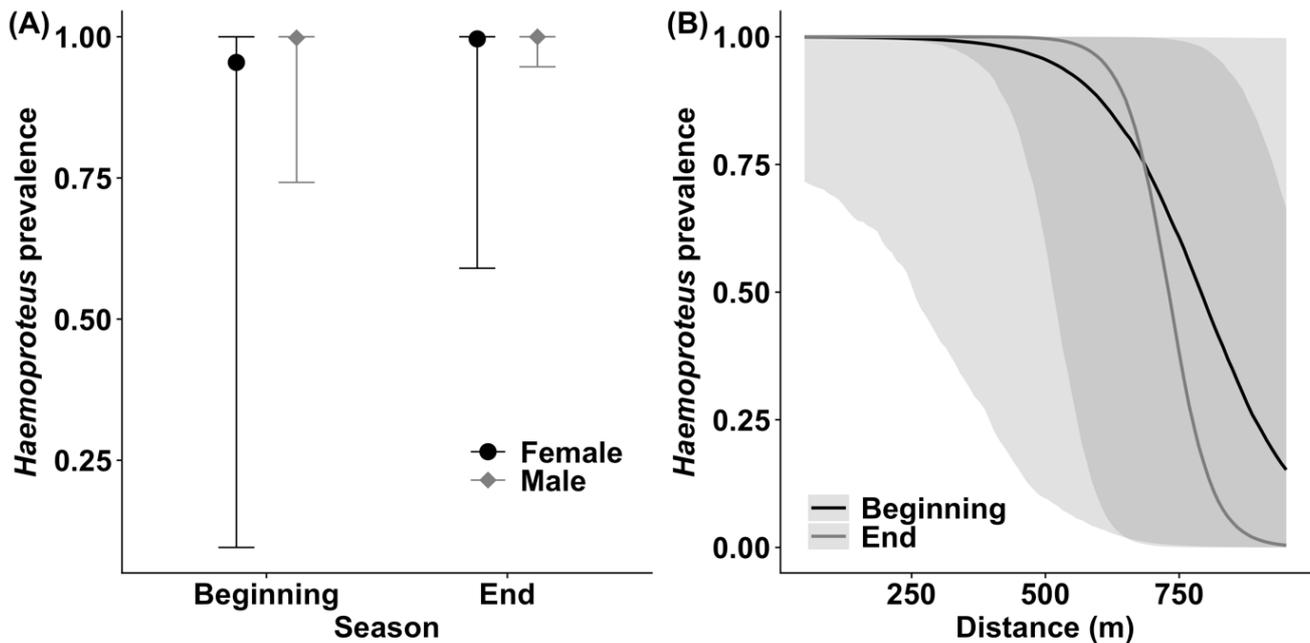


Figure 1. (A) *Haemoproteus* prevalence in the blood of male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (B) The association between the distance from the nearest water bodies and *Haemoproteus* prevalence at the beginning and end of the breeding season. Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals.

Haemoproteus parasitemia did not differ between the sexes (estimate 0.53 , CI: $(-0.16, 1.25)$, Figure 2A). *Haemoproteus* parasitemia significantly increased over the course of the breeding season in both sexes (estimates from -2.686 to -0.918 ; Figure 2A). The distance to the nearest water body had a significant negative effect on *Haemoproteus* parasitemia; it differed between seasons, being more distance-dependent at the end of the breeding season (estimate -0.80 , CI: $(-0.90, -0.69)$; Figure 2B).

3.2. *Plasmodium*

Plasmodium infection prevalence significantly increased from the beginning of the breeding season until its end in female (estimate -7.22 , CI: $(-12.38, -2.94)$; Figure 3A) and male flycatchers (-5.96 , CI: $(-13.08, -1.61)$; Figure 3A). The distance to the nearest water body had a significant effect (estimate -3.37 , CI: $(-7.29, -0.49)$) on *Plasmodium* prevalence at the end of the breeding season (Figure 3B). Interaction between the distance to the nearest water body and sex had no significant effect on *Plasmodium* prevalence (estimate 1.14 , CI: $(-2.31, 4.76)$).

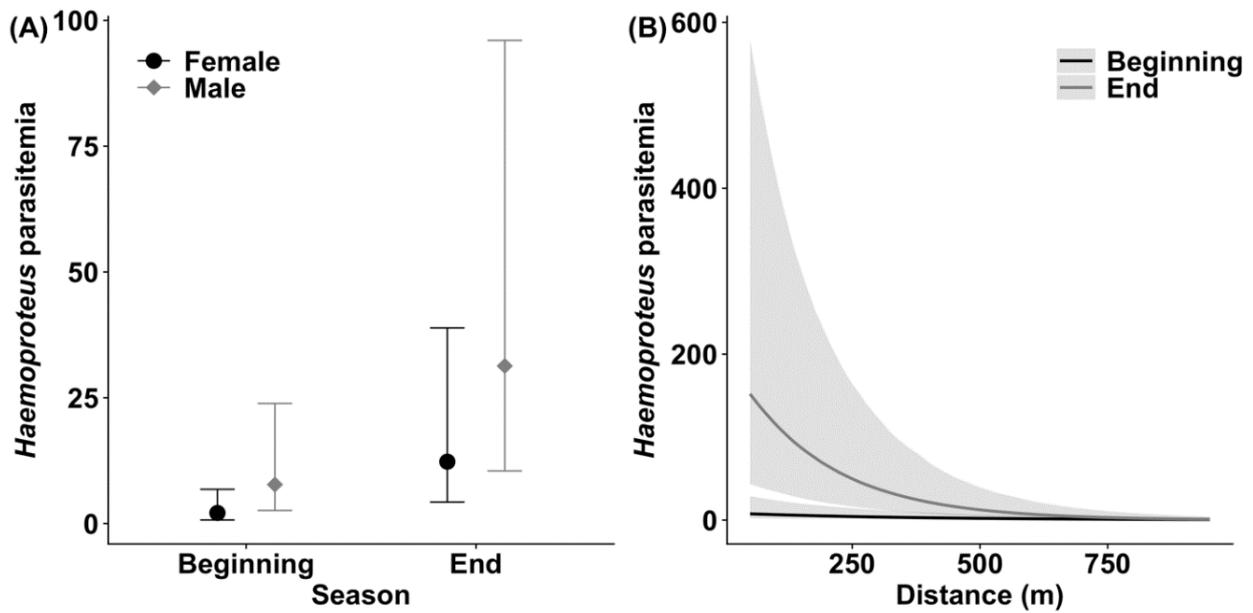


Figure 2. (A) *Haemoproteus* parasitemia in male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (B) The relationship between the *Haemoproteus* parasitemia and the distance to the nearest water bodies at the beginning and the end of the breeding season. Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals.

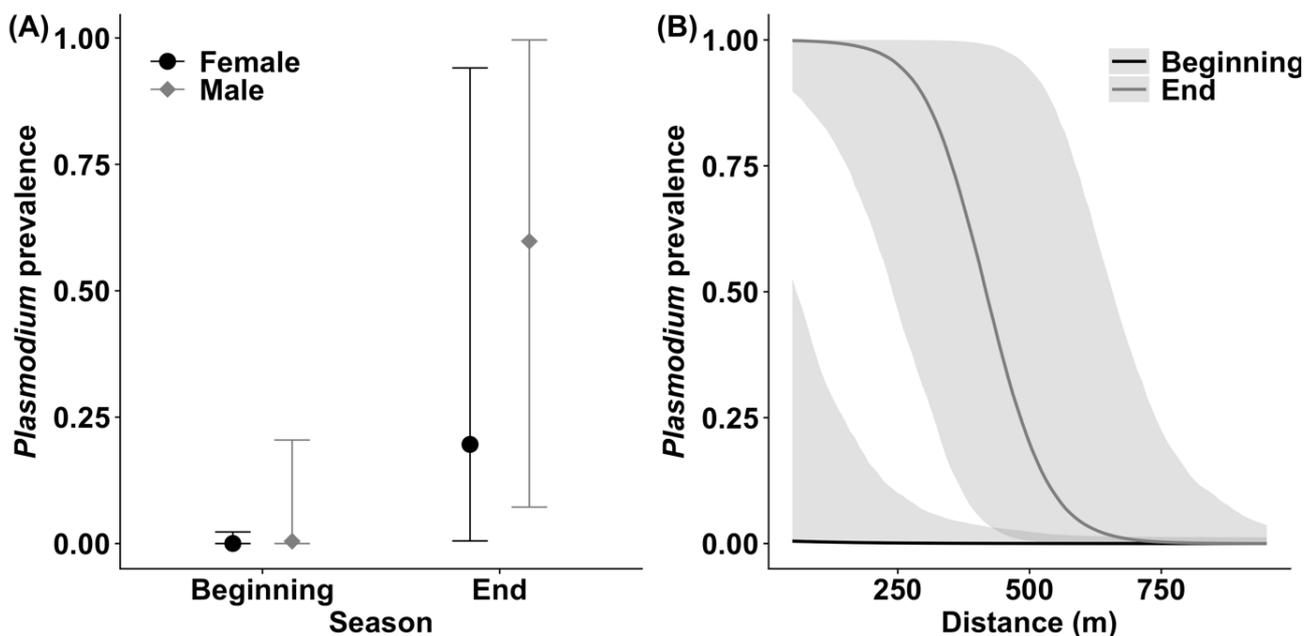


Figure 3. (A) *Plasmodium* prevalence in the blood of male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (B) The relationship between the distance from the nearest water bodies and *Plasmodium* prevalence at the beginning and end of the breeding season. Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals.

Plasmodium parasitemia significantly increased from the beginning to the end of the breeding season in female and male Pied Flycatchers (−2.85, CI: (−4.14, −1.72); Figure 4A). *Plasmodium* parasitemia was not related to the distance to the nearest water body (estimate

–1.51, CI: (–3.27, 0.07); Figure 4B) nor to the interaction between the distance and the season (estimate –1.20, CI: (–2.50, 0.12)) or sex (estimate 0.85, CI: (–0.48, 2.33)).

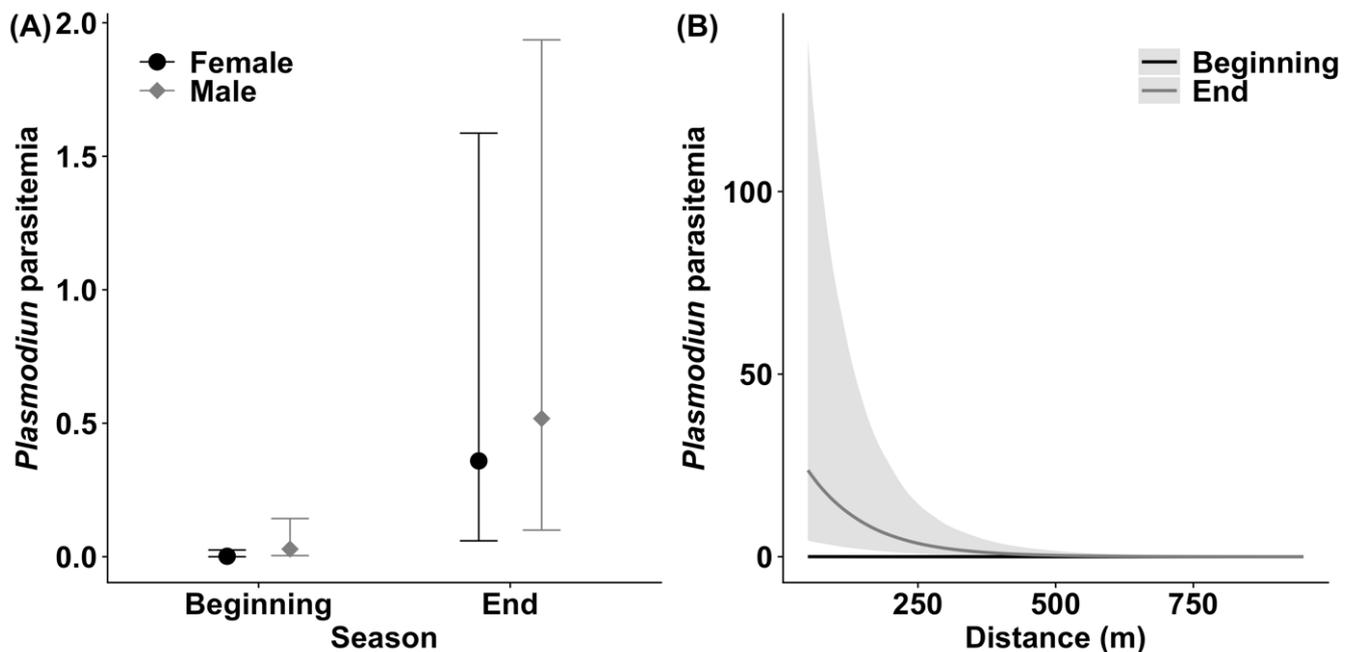


Figure 4. (A) *Plasmodium* parasitemia in male and female Pied Flycatchers at the beginning and end of the breeding season. Error bars represent 95% credibility intervals. (B) The relationship between *Plasmodium* parasitemia and the distance to the nearest water bodies at the beginning and end of the breeding season. Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals.

3.3. Vector Abundance

In total, we trapped 1130 blood-sucking insects (524 biting midges, 575 mosquitoes, and 31 blackflies) that entered 32 nest boxes inhabited by Pied Flycatchers for 7 days. We found a significant negative correlation between the number of parasite vectors and the distance to the nearest water body (Spearman's $r = -0.886$, $n = 32$, $p < 0.0001$, Figure 5).

3.4. Fitness Parameters of Pied Flycatchers

The distance to the nearest water body was not related to clutch size (estimate 0.02, CI: (–0.09, 0.12), Figure 6A). The distance had a positive effect on the fledgling number (estimate 0.13, CI: (0.02, 0.25), Figure 6B). Non-linear effects were observed for the distance to the nearest water body on fledgling body mass (smooth term estimate 7.21, CI: (3.76, 12.39), Figure 6C) and fledgling tarsus length (estimate 0.22, CI: (0.07, 0.55), Figure 6D), but non-significant effects on body condition estimated as residuals from the linear regression of body mass on tarsus length (estimate 0.11, CI: (–0.43, 0.88)). The distance to the nearest water body was not related to adult bird body mass at the beginning of the breeding season (slope estimate 0.01, CI: (–0.04, 0.05)). At the end of the breeding season the distance had a positive effect on adult body mass (slope difference estimate 0.26, CI: (0.21, 0.32)).

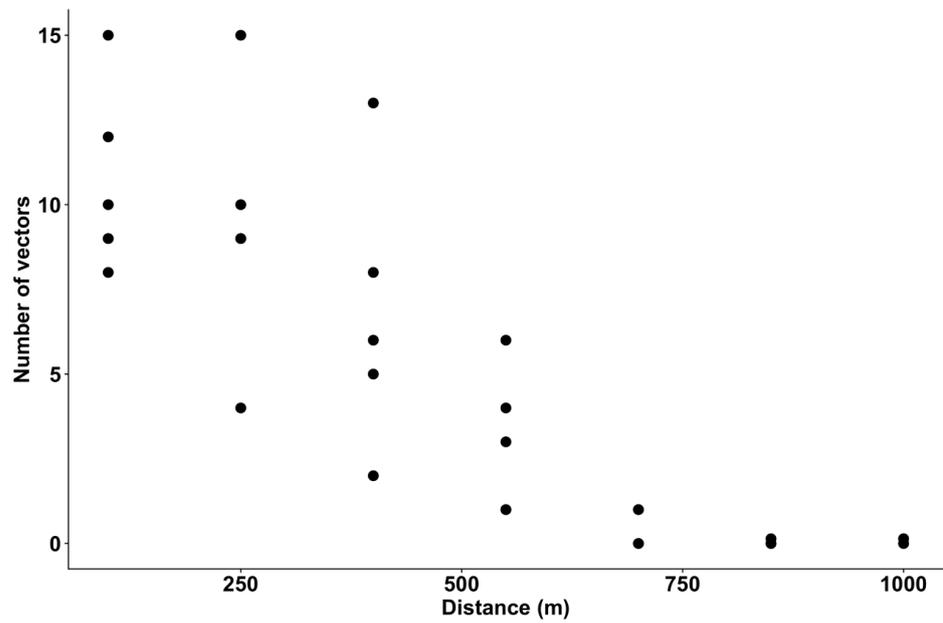


Figure 5. The relationship between the distance to the nearest forest water body and the number of parasite vectors trapped in nest boxes of Pied Flycatchers.

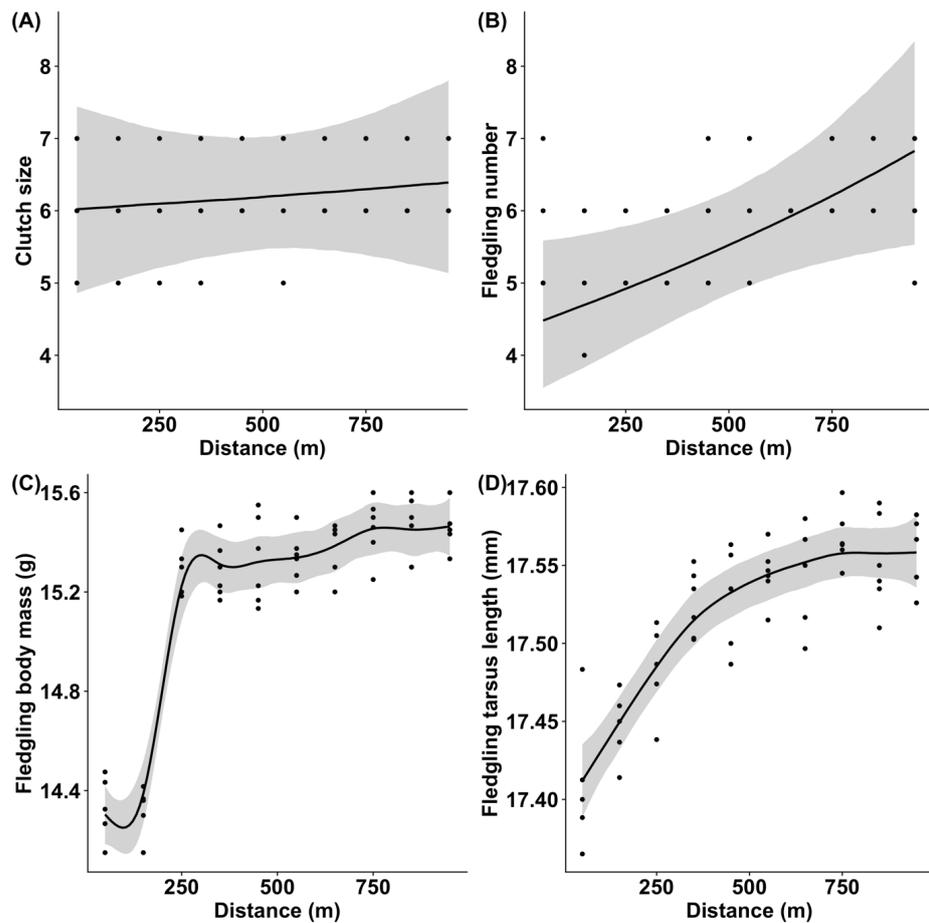


Figure 6. The relationships between the distance to the forest water bodies and clutch size (A), fledgling number (B), fledgling body mass (C), and fledgling tarsus length of Pied Flycatchers (D). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals.

4. Discussion

Overall, our results show that the forests near water bodies constitute an ecological trap for the birds that attempt to breed in these diverse tree stands. Ecological traps arise when organisms mistakenly prefer habitats where their fitness is reduced because they have not experienced such conditions before [52]. Cavities are among the most important cues for habitat selection of cavity-nesting birds [53] and often constitute the only factor limiting their habitat choice. Therefore, Pied Flycatchers can be attracted to breed in almost any type of woodland [54]. Birds can also be attracted to forests near water bodies. The birds may prefer these habitats because of nest box availability, the higher diversity of trees, and the higher numbers of land snails and arthropods [55], while not being able to estimate the risks associated with blood parasite vectors that reproduce in the nearby water bodies. Thus, installing nest boxes near water bodies can lead to fledgling malnutrition, lower survival, and low recruitment rate, suggesting the role of haemosporidian parasites in determining the habitat quality of breeding birds [12,56,57].

This study shows associations between the infection status of individual birds, their condition (body mass) at the end of the breeding season and their fitness parameters estimated with fledgling number, fledgling body mass, and tarsus length. Although infection status at the beginning of the reproductive season and distance from water bodies did not affect clutch size in Pied Flycatchers [58], the fitness of Pied Flycatchers was found to be significantly lower close to forest water bodies such as lakes and bogs. Pied Flycatchers breeding in the vicinity of forest water bodies had fewer and smaller fledglings. Importantly, body mass and body size are reliable predictors of fledgling postnatal survival, because these physical traits are beneficial when escaping predators [59–63].

Haemoproteus and *Plasmodium* parasites cause various adverse physiological and growth effects on their hosts [3,15,27,64,65]. Wild animals show sickness behaviors, which make them more exposed to predation risk, and they are less efficient in finding food during acute stages of haemosporidian infection [3,66]. Although low-grade chronic infections by haemosporidians can persist without direct visible effects on their hosts, recent evidence shows that low-intensity haemosporidian infections may have long-term detrimental effects on the host's physiological condition, the integrity of their genetic material, longevity, and fitness [6]. The results of this study suggest that the infection status of females and males and their abilities to provide parental care are significantly associated, as shown by the number of fledglings and fledgling physical traits.

Human studies have shown that malaria declined rapidly worldwide due to elimination programs that involved draining wetlands [67]. In contrast, environments containing large lakes and lagoons may maintain a high number of malaria vectors [29]. The construction of dams promotes malaria distribution and transmission by providing breeding habitats for malaria vector species [30]. In passerine birds, a few previous studies have already demonstrated a negative relationship between the distance from lakes and streams and the prevalence of haemosporidian parasites during the reproductive season [9,24,27]. This study supports previous research showing that proximity to water bodies generally increases *Haemoproteus* and *Plasmodium* prevalence and parasitemias in breeding birds, which may have detrimental effects on bird longevity and fitness [6].

Importantly, we found that proximity to forest water bodies significantly increased only *Haemoproteus* parasitemia, whereas the intensity of *Plasmodium* infection was not significantly linked with the distance to nearest water body. Evidence suggests that average dispersal distances of mosquitos exceed three km and their flight range is larger than that of biting midges [68], which may explain the results of this study. However, flight distances of blood-sucking insects exhibit large variation and depend on wind direction, wind strength, day and night temperatures, local topography, illumination, humidity, season, and their interactions [68–70], suggesting that more research is needed to elucidate key environmental determinants of vector flights and local distribution.

Although some flycatchers were infected already before their arrival to their breeding grounds [71–73], this study showed that *Haemoproteus* prevalence, *Haemoproteus* para-

sitemia, *Plasmodium* prevalence, and *Plasmodium* parasitemia significantly increased during the breeding season. This shows that *Haemoproteus* and *Plasmodium* parasites mostly infected the breeding Pied Flycatchers during the current reproductive season.

Strikingly, we did not observe any significant differences in parasite prevalence and parasitemias in males and females. In vertebrates, males have often been observed to have higher parasite infection levels relative to females [74,75]. Evidence suggests that sex hormones influence the immune system of breeding individuals, which affects their susceptibility to parasites [76,77]. In passerine birds, females often invest disproportionately more in building nests and incubation than males [78], which impairs the cell-mediated immune system in females [79]. On the other hand, male Pied Flycatchers often practice a mixed-mating system involving attempts to acquire a secondary female to breed with [80]. This costly investment into reproduction may exacerbate cell-mediated and humoral immunity in males [79], leading to similar infection rates in female and male Pied Flycatchers.

We did not estimate the amount of food resources available to the birds in this study. However, our previous studies showed that tree diversity affects food resource availability to small passerines [38,81]. Canopy, subcanopy, sapling, and shrub strata were recorded in all forest plots near water bodies, whereas only canopy and sparse shrub strata were available to the birds in the remote breeding areas. Besides having the highest tree diversity, areas near forest lakes and streams are usually more diverse in snails and slugs, which are important calcium sources during egg production for birds [82,83]. Thus, despite choosing the highest quality habitats possible, Pied Flycatchers had higher haemosporidian prevalence and the most intense parasitemias, the lowest adult body mass at the end of the breeding season, the lowest number of fledglings, and the worst-condition fledglings when breeding near forest water bodies.

This study has some drawbacks. First, the nest boxes were closed until the end of April to prevent them from being occupied by Great Tits. Although this approach allowed us to remove the factor of interspecific competition from our study system, we probably did not allow some older (2nd calendar year and older) males to settle in the study area. However, we did not affect the age structure of female flycatchers because the nest box entrances were opened a number of days before females arrived. Second, we could not discriminate between local blood parasites and parasites acquired during migration and the winter season using the microscopy approach, and, therefore, future studies must be based on molecular methods. This is crucial not only to confirm the current results but also to disentangle the physiological and ecological effects caused by blood parasites of different origins. Third, the research of this kind needs to cover more breeding seasons of birds to avoid any possible natural variation in population numbers of hosts and parasites.

5. Conclusions

Our study provides evidence on an overlooked issue affecting reproductive success in forest passerine birds by showing that haemosporidian parasites affect their hosts' fitness and turn large forest areas around water bodies into ecological traps. This ecosystem property must be considered when planning investments in the conservation of a species vulnerable to infections of haemosporidian parasites, as these powerful parasites may ruin conservation attempts by creating unintended ecological traps around forest water bodies [52].

Author Contributions: R.K., T.K., I.A.K., J.D. and G.B. conceived and designed the study and participated in the drafting of the manuscript. R.K., T.K., J.D., G.B., L.S., I.D. and I.A.K. performed the study, collected and extracted data. R.K., T.K., P.R., G.B., D.E. and I.A.K. analyzed data. L.S. and I.D. participated in data and drafting the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by the Latvian Council of Science (grants lzp-2018/2-00057, lzp-2020/2-0271 and lzp-2021/1-0277), and the Estonian Research Council (grant PUT1223).

Institutional Review Board Statement: The research protocol was approved by the Food and Veterinary Agency of the Republic of Latvia (permission number 88).

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Kristeris-Raivo Krams for his help with taking measurements and Severi Luoto for improving the style of our language, and for valuable comments.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Schmid-Hempel, P. *Evolutionary Parasitology: The Integrated Study of Infections, Immunology, Ecology, and Genetics*; Oxford University Press: New York, NY, USA, 2011.
- Svensson-Coelho, M.; Ricklefs, R.E. Host Phylogeography and Beta Diversity in Avian Haemosporidian (Plasmodiidae) Assemblages of the Lesser Antilles: Haemosporidian Beta Diversity and Host Phylogeography. *J. Anim. Ecol.* **2011**, *80*, 938–946. [[CrossRef](#)] [[PubMed](#)]
- Krams, I.A.; Suraka, V.; Rantala, M.J.; Sepp, T.; Mierauskas, P.; Vrublevska, J.; Krama, T. Acute Infection of Avian Malaria Impairs Concentration of Haemoglobin and Survival in Juvenile Altricial Birds: Costs of Malaria Infection. *J. Zool.* **2013**, *291*, 34–41. [[CrossRef](#)]
- García-Longoria, L.; Garamszegi, L.Z.; Møller, A.P. Host Escape Behavior and Blood Parasite Infections in Birds. *Behav. Ecol.* **2014**, *25*, 890–900. [[CrossRef](#)]
- Heil, M. Host Manipulation by Parasites: Cases, Patterns, and Remaining Doubts. *Front. Ecol. Evol.* **2016**, *4*, 80. [[CrossRef](#)]
- Asghar, M.; Hasselquist, D.; Hansson, B.; Zehtindjiev, P.; Westerdahl, H.; Bensch, S. Hidden Costs of Infection: Chronic Malaria Accelerates Telomere Degradation and Senescence in Wild Birds. *Science* **2015**, *347*, 436–438. [[CrossRef](#)] [[PubMed](#)]
- Krama, T.; Krams, R.; Cīrule, D.; Moore, F.R.; Rantala, M.J.; Krams, I.A. Intensity of Haemosporidian Infection of Parids Positively Correlates with Proximity to Water Bodies, but Negatively with Host Survival. *J. Ornithol.* **2015**, *156*, 1075–1084. [[CrossRef](#)]
- Rätti, O.; Dufva, R.; Alatalo, R.V. Blood Parasites and Male Fitness in the Pied Flycatcher. *Oecologia* **1993**, *96*, 410–414. [[CrossRef](#)]
- Krams, I.; Suraka, V.; Rattiste, K.; Āboliņš-Ābols, M.; Krama, T.; Rantala, M.J.; Mierauskas, P.; Cīrule, D.; Saks, L. Comparative Analysis Reveals a Possible Immunity-Related Absence of Blood Parasites in Common Gulls (*Larus canus*) and Black-Headed Gulls (*Chroicocephalus ridibundus*). *J. Ornithol.* **2012**, *153*, 1245–1252. [[CrossRef](#)]
- Martínez-de la Puente, J.; Martínez, J.; Rivero-De-Aguilar, J.; Del Cerro, S.; Merino, S. Vector Abundance Determines Trypanosoma Prevalence in Nestling Blue Tits. *Parasitology* **2013**, *140*, 1009–1015. [[CrossRef](#)]
- Ferraguti, M.; Martínez-de la Puente, J.; Bensch, S.; Roiz, D.; Ruiz, S.; Viana, D.S.; Soriguer, R.C.; Figuerola, J. Ecological Determinants of Avian Malaria Infections: An Integrative Analysis at Landscape, Mosquito and Vertebrate Community Levels. *J. Anim. Ecol.* **2018**, *87*, 727–740. [[CrossRef](#)]
- Gonzalez-Quevedo, C.; Davies, R.G.; Richardson, D.S. Predictors of Malaria Infection in a Wild Bird Population: Landscape-Level Analyses Reveal Climatic and Anthropogenic Factors. *J. Anim. Ecol.* **2014**, *83*, 1091–1102. [[CrossRef](#)] [[PubMed](#)]
- Piersma, T. Do Global Patterns of Habitat Use and Migration Strategies Co-Evolve with Relative Investments in Immunocompetence Due to Spatial Variation in Parasite Pressure? *Oikos* **1997**, *80*, 623. [[CrossRef](#)]
- Warner, R.E. The Role of Introduced Diseases in the Extinction of the Endemic Hawaiian Avifauna. *Condor* **1968**, *70*, 101–120. [[CrossRef](#)]
- van Riper, C.; van Riper, S.G.; Goff, M.L.; Laird, M. The Epizootiology and Ecological Significance of Malaria in Hawaiian Land Birds. *Ecol. Monogr.* **1986**, *56*, 327–344. [[CrossRef](#)]
- Little, R.M.; Earlé, R.A. Sandgrouse (Pterocleididae) and Sociable Weavers Philetarius Socius Lack Avian Haematozoa in Semi-Arid Regions of South Africa. *J. Arid Environ.* **1995**, *30*, 367–370. [[CrossRef](#)]
- Figuerola, J. Effects of Salinity on Rates of Infestation of Waterbirds by Haematozoa. *Ecography* **1999**, *22*, 681–685. [[CrossRef](#)]
- Sol, D.; Jovani, R.; Torres, J. Geographical Variation in Blood Parasites in Feral Pigeons: The Role of Vectors. *Ecography* **2000**, *23*, 307–314. [[CrossRef](#)]
- Hellgren, O.; Bensch, S.; Malmqvist, B. Bird Hosts, Blood Parasites and Their Vectors—Associations Uncovered by Molecular Analyses of Blackfly Blood Meals. *Mol. Ecol.* **2008**, *17*, 1605–1613. [[CrossRef](#)]
- Arriero, E.; Moreno, J.; Merino, S.; Martínez, J. Habitat Effects on Physiological Stress Response in Nestling Blue Tits Are Mediated through Parasitism. *Physiol. Biochem. Zool.* **2008**, *81*, 195–203. [[CrossRef](#)]
- Arriero, E. Rearing Environment Effects on Immune Defence in Blue Tit *Cyanistes caeruleus* Nestlings. *Oecologia* **2009**, *159*, 697–704. [[CrossRef](#)]
- Sehgal, R.N.M. Deforestation and Avian Infectious Diseases. *J. Exp. Biol.* **2010**, *213*, 955–960. [[CrossRef](#)] [[PubMed](#)]
- Kettle, D. *Medical and Veterinary Entomology*; CAB International: Wallingford, UK, 1995.
- Wood, M.J.; Cosgrove, C.L.; Wilkin, T.A.; Knowles, S.C.L.; Day, K.P.; Sheldon, B.C. Within-Population Variation in Prevalence and Lineage Distribution of Avian Malaria in Blue Tits, *Cyanistes caeruleus*: Within-population variation in blue tit malaria. *Mol. Ecol.* **2007**, *16*, 3263–3273. [[CrossRef](#)] [[PubMed](#)]

25. Ishtiaq, F.; Guillaumot, L.; Clegg, S.M.; Phillimore, A.B.; Black, R.A.; Owens, I.P.F.; Mundy, N.I.; Sheldon, B.C. Avian Haematozoan Parasites and Their Associations with Mosquitoes across Southwest Pacific Islands. *Mol. Ecol.* **2008**, *17*, 4545–4555. [[CrossRef](#)] [[PubMed](#)]
26. Njabo, K.Y.; Cornel, A.J.; Sehgal, R.N.; Loiseau, C.; Buermann, W.; Harrigan, R.J.; Pollinger, J.; Valkiūnas, G.; Smith, T.B. Coquillettidia (Culicidae, Diptera) Mosquitoes Are Natural Vectors of Avian Malaria in Africa. *Malar. J.* **2009**, *8*, 193. [[CrossRef](#)]
27. Krams, I.; Cīrule, D.; Krama, T.; Hukkanen, M.; Rytönen, S.; Orell, M.; Iezhova, T.; Rantala, M.J.; Tummelleht, L. Effects of Forest Management on Haematological Parameters, Blood Parasites, and Reproductive Success of the Siberian Tit (*Poecile cinctus*) in Northern Finland. *Ann. Zool. Fenn.* **2010**, *47*, 335–346. [[CrossRef](#)]
28. Santiago-Alarcon, D.; Palinauskas, V.; Schaefer, H.M. Diptera Vectors of Avian Haemosporidian Parasites: Untangling Parasite Life Cycles and Their Taxonomy. *Biol. Rev.* **2012**, *87*, 928–964. [[CrossRef](#)]
29. Minakawa, N.; Dida, G.O.; Sonye, G.O.; Futami, K.; Njenga, S.M. Malaria Vectors in Lake Victoria and Adjacent Habitats in Western Kenya. *PLoS ONE* **2012**, *7*, e32725. [[CrossRef](#)]
30. Kibret, S.; Wilson, G.G.; Ryder, D.; Tekie, H.; Petros, B. The Influence of Dams on Malaria Transmission in Sub-Saharan Africa. *EcoHealth* **2017**, *14*, 408–419. [[CrossRef](#)]
31. Valkiūnas, G. *Avian Malaria Parasites and Other Haemosporidia*; CRC Press: Boca Raton, FL, USA, 2005.
32. Kim, K.S.; Tsuda, Y.; Yamada, A. Bloodmeal Identification and Detection of Avian Malaria Parasite From Mosquitoes (Diptera: Culicidae) Inhabiting Coastal Areas of Tokyo Bay, Japan. *J. Med. Entomol.* **2009**, *46*, 1230–1234. [[CrossRef](#)]
33. Ferraguti, M.; Martínez-de la Puente, J.; Muñoz, J.; Roiz, D.; Ruiz, S.; Soriguer, R.; Figuerola, J. Avian Plasmodium in Culex and Ochlerotatus Mosquitoes from Southern Spain: Effects of Season and Host-Feeding Source on Parasite Dynamics. *PLoS ONE* **2013**, *8*, e66237. [[CrossRef](#)]
34. Ferraguti, M.; Martínez-de la Puente, J.; Ruiz, S.; Soriguer, R.; Figuerola, J. On the Study of the Transmission Networks of Blood Parasites from SW Spain: Diversity of Avian Haemosporidians in the Biting Midge Culicoides Circumscriptus and Wild Birds. *Parasites Vectors* **2013**, *6*, 208. [[CrossRef](#)] [[PubMed](#)]
35. Hendry, G. *Midges in Scotland*; Aberdeen University Press: Aberdeen, UK, 1989.
36. Both, C.; Bijlsma, R.G.; Visser, M.E. Climatic Effects on Timing of Spring Migration and Breeding in a Long-Distance Migrant, the Pied Flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* **2005**, *36*, 368–373. [[CrossRef](#)]
37. Goffin, B.; Felgueiras, M.; Hof, A.R. Increased Stopover Duration and Low Body Condition of the Pied Flycatcher (*Ficedula hypoleuca*) at an Autumn Stopover Site. *Animals* **2020**, *10*, 2208. [[CrossRef](#)] [[PubMed](#)]
38. Rytönen, S.; Krams, I. Does Foraging Behaviour Explain the Poor Breeding Success of Great Tits *Parus major* in Northern Europe? *J. Avian Biol.* **2003**, *34*, 288–297. [[CrossRef](#)]
39. Brūmelis, G.; Dauškane, I.; Elferts, D.; Strode, L.; Krama, T.; Krams, I. Estimates of Tree Canopy Closure and Basal Area as Proxies for Tree Crown Volume at a Stand Scale. *Forests* **2020**, *11*, 1180. [[CrossRef](#)]
40. Ruuskanen, S.; Siitari, H.; Eeva, T.; Belskii, E.; Järvinen, A.; Kerimov, A.; Krams, I.; Moreno, J.; Morosinotto, C.; Mänd, R.; et al. Geographical Variation in Egg Mass and Egg Content in a Passerine Bird. *PLoS ONE* **2011**, *6*, e25360. [[CrossRef](#)]
41. Samplonius, J.M.; Bartošová, L.; Burgess, M.D.; Bushuev, A.V.; Eeva, T.; Ivankina, E.V.; Kerimov, A.B.; Krams, I.; Laaksonen, T.; Mägi, M.; et al. Phenological Sensitivity to Climate Change Is Higher in Resident than in Migrant Bird Populations among European Cavity Breeders. *Glob. Chang. Biol.* **2018**, *24*, 3780–3790. [[CrossRef](#)]
42. Lundberg, A.; Alatalo, R.V. *The Pied Flycatcher*; T & AD Poyser: London, UK, 1992.
43. Ojanen, M. A Method for Age Determination of Pied Flycatchers *Ficedula hypoleuca* in Spring. *Acta Regiae Soc. Sci. Litt. Gothobg. Zool.* **1987**, *14*, 95–101.
44. Forsman, J.T.; Seppänen, J.-T.; Mönkkönen, M.; Thomson, R.L.; Kivelä, S.M.; Krams, I.; Loukola, O.J. Is It Interspecific Information Use or Aggression between Putative Competitors That Steers the Selection of Nest-Site Characteristics? A Reply to Slagsvold and Wiebe. *J. Avian Biol.* **2018**, *49*, jav-01558. [[CrossRef](#)]
45. Loukola, O.J.; Seppänen, J.-T.; Krams, I.; Torvinen, S.S.; Forsman, J.T. Observed Fitness May Affect Niche Overlap in Competing Species via Selective Social Information Use. *Am. Nat.* **2013**, *182*, 474–483. [[CrossRef](#)]
46. Bennett, G.F. Simple Techniques for Making Avian Blood Smears. *Can. J. Zool.* **1970**, *48*, 585–586. [[CrossRef](#)]
47. Bennett, G.F.; Siikamäki, P.; Jokimäki, J.; Hovi, M.; Huhta, E. Leucocytozoon Muscipapa n. Sp. (Leucocytozoidae: Apicomplexa) from the Pied Flycatcher *Ficedula hypoleuca* (Pallas) (Passeriformes: Muscipapinae). *Syst. Parasitol.* **1995**, *31*, 33–36. [[CrossRef](#)]
48. Rintamäki, P.T.; Huhta, E.; Jokimäki, J.; Squires-Parsons, D. Leucocytozoonosis and Trypanosomiasis in Redstarts in Finland. *J. Wildl. Dis.* **1999**, *35*, 603–607. [[CrossRef](#)] [[PubMed](#)]
49. Schulte-Hostedde, A.I.; Zinner, B.; Millar, J.S.; Hickling, G.J. Restitution of Mass-Size Residuals: Validating Body Condition Indices. *Ecology* **2005**, *86*, 155–163. [[CrossRef](#)]
50. R Core Team. *A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020; Available online: <https://www.R-project.org/> (accessed on 3 April 2022).
51. Bürkner, P.-C. Brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **2017**, *80*, 1–28. [[CrossRef](#)]
52. Hale, R.; Swearer, S.E. Ecological Traps: Current Evidence and Future Directions. *Proc. R. Soc. B.* **2016**, *283*, 20152647. [[CrossRef](#)] [[PubMed](#)]
53. Hildén, O. Habitat Selection in Birds: A Review. *Ann. Zool. Fenn.* **1965**, *2*, 53–75.

54. Mägi, M.; Mänd, R.; Tamm, H.; Sisask, E.; Kilgas, P.; Tilgar, V. Low Reproductive Success of Great Tits in the Preferred Habitat: A Role of Food Availability. *Écoscience* **2009**, *16*, 145–157. [[CrossRef](#)]
55. Jokimäki, J.; Huhta, E.; Itämies, J.; Rahko, P. Distribution of Arthropods in Relation to Forest Patch Size, Edge, and Stand Characteristics. *Can. J. For. Res.* **1998**, *28*, 1068–1072. [[CrossRef](#)]
56. Muriel, J.; Marzal, A.; Magallanes, S.; García-Longoria, L.; Suarez-Rubio, M.; Bates, P.J.J.; Lin, H.H.; Soe, A.N.; Oo, K.S.; Aye, A.A.; et al. Prevalence and Diversity of Avian Haemosporidians May Vary with Anthropogenic Disturbance in Tropical Habitats in Myanmar. *Diversity* **2021**, *13*, 111. [[CrossRef](#)]
57. Illera, J.C.; López, G.; García-Padilla, L.; Moreno, Á. Factors Governing the Prevalence and Richness of Avian Haemosporidian Communities within and between Temperate Mountains. *PLoS ONE* **2017**, *12*, e0184587. [[CrossRef](#)] [[PubMed](#)]
58. Dale, S.; Kruszewicz, A.; Slagsvold, T. Effects of Blood Parasites on Sexual and Natural Selection in the Pied Flycatcher. *J. Zool.* **1996**, *238*, 373–393. [[CrossRef](#)]
59. Magrath, R.D. Nestling Weight and Juvenile Survival in the Blackbird, *Turdus merula*. *J. Anim. Ecol.* **1991**, *60*, 335. [[CrossRef](#)]
60. Naef-Daenzer, B.; Keller, L.F. The Foraging Performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in Relation to Caterpillar Development, and Its Consequences for Nestling Growth and Fledging Weight. *J. Anim. Ecol.* **1999**, *68*, 708–718. [[CrossRef](#)]
61. Gruebler, M.U.; Naef-Daenzer, B. Survival Benefits of Post-Fledging Care: Experimental Approach to a Critical Part of Avian Reproductive Strategies. *J. Anim. Ecol.* **2010**, *79*, 334–341. [[CrossRef](#)] [[PubMed](#)]
62. Gruebler, M.U.; Naef-Daenzer, B. Fitness Consequences of Timing of Breeding in Birds: Date Effects in the Course of a Reproductive Episode. *J. Avian Biol.* **2010**, *41*, 282–291. [[CrossRef](#)]
63. Naef-Daenzer, B.; Gruebler, M.U. Post-fledging Survival of Altricial Birds: Ecological Determinants and Adaptation. *J. Field Ornithol.* **2016**, *87*, 227–250. [[CrossRef](#)]
64. Sheldon, B.C.; Verhulst, S. Ecological Immunology: Costly Parasite Defences and Trade-Offs in Evolutionary Ecology. *Trends Ecol. Evol.* **1996**, *11*, 317–321. [[CrossRef](#)]
65. Marzal, A.; de Lope, F.; Navarro, C.; Møller, A.P. Malarial Parasites Decrease Reproductive Success: An Experimental Study in a Passerine Bird. *Oecologia* **2005**, *142*, 541–545. [[CrossRef](#)]
66. Gutiérrez-López, R.; Gangoso, L.; Martínez-de la Puente, J.; Fric, J.; López-López, P.; Maillieux, M.; Muñoz, J.; Touati, L.; Samraoui, B.; Figuerola, J. Low Prevalence of Blood Parasites in a Long-Distance Migratory Raptor: The Importance of Host Habitat. *Parasites Vectors* **2015**, *8*, 189. [[CrossRef](#)]
67. Piperaki, E.T.; Daikos, G.L. Malaria in Europe: Emerging Threat or Minor Nuisance? *Clin. Microbiol. Infect.* **2016**, *22*, 487–493. [[CrossRef](#)] [[PubMed](#)]
68. Elbers, A.R.W.; Koenraadt, C.; Meiswinkel, R. Mosquitoes and Culicoides Biting Midges: Vector Range and the Influence of Climate Change: -EN- -FR- Les Moustiques et Les Moucheron Piqueurs Culicoïdes: Diversité Des Vecteurs et Influence Du Changement Climatique -ES- Mosquitos y Jenes Culicoïdes: Distribución de Los Vectores e Influencia Del Cambio Climático. *Rev. Sci. Tech. OIE* **2015**, *34*, 123–137. [[CrossRef](#)]
69. Brand, S.P.C.; Keeling, M.J. The Impact of Temperature Changes on Vector-Borne Disease Transmission: Culicoides Midges and Bluetongue Virus. *J. R. Soc. Interface* **2017**, *14*, 20160481. [[CrossRef](#)] [[PubMed](#)]
70. Kluiters, G.; Swales, H.; Baylis, M. Local Dispersal of Palaearctic Culicoides Biting Midges Estimated by Mark-Release-Recapture. *Parasit Vectors* **2015**, *8*, 86. [[CrossRef](#)] [[PubMed](#)]
71. Wiersch, S.C.; Lubjuhn, T.; Maier, W.A.; Kampen, H. Haemosporidian Infection in Passerine Birds from Lower Saxony. *J. Ornithol.* **2007**, *148*, 17–24. [[CrossRef](#)]
72. Dubiec, A.; Podmokła, E.; Harnist, I.; Mazgajski, T.D. Haemoparasites of the Pied Flycatcher: Inter-Population Variation in the Prevalence and Community Composition. *Parasitology* **2018**, *145*, 912–919. [[CrossRef](#)]
73. Jones, W.; Kulma, K.; Bensch, S.; Cichoń, M.; Kerimov, A.; Krist, M.; Laaksonen, T.; Moreno, J.; Munclinger, P.; Slater, F.M.; et al. Interspecific Transfer of Parasites Following a Range-Shift in Ficedula Flycatchers. *Ecol. Evol.* **2018**, *8*, 12183–12192. [[CrossRef](#)]
74. Zuk, M.; McKean, K.A. Sex Differences in Parasite Infections: Patterns and Processes. *Int. J. Parasitol.* **1996**, *26*, 1009–1024. [[CrossRef](#)]
75. Calero-Riestra, M.; García, J.T. Sex-Dependent Differences in Avian Malaria Prevalence and Consequences of Infections on Nestling Growth and Adult Condition in the Tawny Pipit, *Anthus campestris*. *Malar. J.* **2016**, *15*, 178. [[CrossRef](#)]
76. Grossman, C. Possible Underlying Mechanisms of Sexual Dimorphism in the Immune Response, Fact and Hypothesis. *J. Steroid Biochem.* **1989**, *34*, 241–251. [[CrossRef](#)]
77. Folstad, I.; Karter, A.J. Parasites, Bright Males, and the Immunocompetence Handicap. *Am. Nat.* **1992**, *139*, 603–622. [[CrossRef](#)]
78. Ots, I.; Hórák, P. Great Tits *Parus major* Trade Health for Reproduction. *Proc. R. Soc. B Biol. Sci.* **1996**, *263*, 1443–1447.
79. Grossman, C. Interactions between the Gonadal Steroids and the Immune System. *Science* **1985**, *227*, 257–261. [[CrossRef](#)] [[PubMed](#)]
80. Alatalo, R.V.; Lundberg, A. Polyterritorial Polygyny in the Pied Flycatcher. In *Advances in the Study of Behavior*; Elsevier: Amsterdam, The Netherlands, 1990; Volume 19, pp. 1–27, ISBN 978-0-12-004519-8.
81. Krams, I.; Krams, T.; Cernihovics, J. Selection of Foraging Sites in Mixed Willow and Crested Tit Flocks: Rank-Dependent Survival Strategies. *Ornis Fenn.* **2001**, *78*, 1–11.
82. Mänd, R.; Tilgar, V.; Leivits, A. Calcium, Snails, and Birds: A Case Study. *Web Ecol.* **2000**, *1*, 63–69. [[CrossRef](#)]
83. Dhondt, A.A.; Hochachka, W.M. Variations in Calcium Use by Birds During the Breeding Season. *Condor* **2001**, *103*, 592–598. [[CrossRef](#)]