DAUGAVPILS UNIVERSITY
INSTITUTE OF LIFE SCIENCES AND TECHNOLOGY
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LABORATORY OF ANIMAL ECOLOGY AND EVOLUTION

RONALDS KRAMS

THE ROLE OF ECOLOGICAL TRAPS IN BIRD SURVIVAL AND REPRODUCTION

EKOLOĢISKO SLAZDU IETEKME UZ PUTNU IZDZĪVOŠANU UN VAIROŠANOS

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Supervisor:
Dr. biol., senior researcher, prof. Indriķis Krams
Scientific advisor:
Dr. biol., senior researcher Tatjana Krama

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Supervisor:
Dr. biol., senior researcher, prof. Indriķis Krams
Scientific advisor:
Dr. biol., senior researcher Tatjana Krama

Opponents:
1. Ph. D., researcher Rolands Moisejevs (Daugavpils University);
2. Dr. med. vet., senior researcher, prof. Aivars Bērziņš (Institute of Food safety, Animal Health and Environment “BIOR”);
3. Ph. D., prof. Pranas Mierauskas (Mykolo Romerio universitetas / Mykolas Romeris University, Vilnius, Lithuania).

Chairman of the Promotion Board:
Dr. biol., prof. Arvīds Barševskis

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Send feedback: to the Secretary of the Promotion Board, Daugavpils University researcher, Dr. biol. Jana Paidere, Parādes street 1A, Daugavpils, Latvia, LV-5401; Tel. +37126002593, e-mail: jana.paidere@du.lv

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Promocijas darba zinātniskais vadītājs:
Dr. biol., vadošais pētnieks, prof. Indriķis Krams
Promocijas darba zinātniskais konsultants:
Dr. biol., vadošā pētniece Tatjana Krama

Darba recenzenti:
1. Ph. D., pētnieks Rolands Moisejevs (Daugavpils Universitāte);
2. Dr. med. vet., vadošais pētnieks, prof. Aivars Bērziņš (Pārtikas drošības, dzīvnieku veselības un vides zinātniskais institūts “BIOR”);
3. Ph. D., prof. Pranas Mierauskas (Mykolo Romerio universitetas / Mikola Romera universitāte, Viļņa, Lietuva).

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Dr. biol., prof. Arvīds Barševskis

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I. **Krams, R.**, Krama, T., Brūmelis, G., Elferts, D., Strode, L., Dauškane, I., Luoto, S., Šmits, A. & Krams, I.A. (2021). Ecological traps: evidence of a fitness cost in a cavity-nesting bird. *Oecologia*, 196(3): 735–745. DOI: 10.1007/s00442-021-04969-w.

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III. Krama, T., **Krams, R.**, Cīrule, D., Moore, F.R., Rantala, M.J. & Krams, I.A. (2015). Intensity of haemosporidian infection of parids positively correlates with proximity to water bodies, but negatively with host survival. *Journal of Ornithology*, 156(4):1075–1084. DOI: 10.1007/s10336-015-1206-5.

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5. *The 64th International Scientific Conference of Daugavpils University*, Daugavpils, 21.04.–22.04.2022., workgroup "Biology", oral presentation "Proximity to water bodies effect on the blood parasite infection rate, reproduction and fitness of the European Pied Flycatcher (*Ficedula hypoleuca* Pallas, 1764)", **R. Krams**, T. Krama, D. Elferts, J. Daukšte, P. Raibarte, G. Brūmelis, I. Dauškane, L. Strode, I. Krams.

6. *80th International Scientific Conference of the University of Latvia*, Rīga, 03.02.2022., workgroup "Innovative and Applied Research in Biology", oral presentation "Reproductive success of the great tit (*Parus major* Linnaeus, 1758) under ecological trap conditions", **R. Krams**, T. Krama, G. Brūmelis, D. Elferts, L. Strode, I. Dauškane, A. Šmits, I. Krams.

7. *80th International Scientific Conference of the University of Latvia*, Rīga, 03.02.2022., workgroup “Zoology and Animal Ecology”, oral presentation “Outbreaks of the great web-spinning sawfly (*Acantholyda posticalis* Matsumura, 1912) effect on the reproductive success of great tits (*Parus major Linnaeus*, 1758)”, **R. Krams**, T. Krama, G. Brūmelis, D. Elferts, L. Strode, I. Dauškane, A. Šmits, I. Krams.

8. *8th International Conference on Biodiversity Research*, Daugavpils, 28.04. – 30.04.2015., section “Biodiversity of parasites and their hosts”, poster presentation “Relationship between water body proximity and blood parasite prevalence in crested tits (*Lophophanes cristatus*) and willow tits (*Poecile montanus*)”, **R. Krams**, T. Krama, J. Vrubļevska, S. Kecko, I. Skrinda, I. Krams.

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1. INTRODUCTION

1.1. Habitat selection

When an animal selects an area to reproduce, overwinter or migrate, it often chooses a specific habitat based on a particular combination of features available in that type of area. A habitat is supposed to meet all the environmental requirements an organism needs to survive or increase its fitness. Habitats differ between species and populations as their requirements may differ. Therefore, the concept of habitat sharply differs from other fundamental ecological concepts such as environment or just a set of specific environmental conditions found in a particular area (Cody 1985; Krausman & Morrison 2016). The term habitat reflects the species requirements consisting of various abiotic and biotic factors and resources occurring in the area. Notably, the habitat of a species has been considered the hypervolume of its ecological and physiological requirements, called ecological niche (Hutchinson 1957). Odum and Barrett (2004) included in the term ecological niche also such essential components as morphological, anatomical and physiological adaptations and behavioural responses required to find or choose proper species-specific habitat. Odum and Barrett (2004) suggested defining the organism's habitat as its "address", while they called the ecological niche the "profession" of the organisms or species.

Habitat selection is a dynamic decision-making process, and evidence suggests that animals base their decisions on a number of environmental cues to evaluate the present condition of habitat quality and its possible changes in time (Demeyrier *et al.* 2016). Habitat choice is of crucial importance because only the correct choices decrease uncertainty about habitat quality and improve the fitness of organisms. To decrease uncertainty and improve habitat choice, organisms must acquire and process information about habitat properties (Szymkowiak 2013). However, it is doubtful if organisms can acquire and use all available information over short periods of time, especially in seasonal environments, to make proper decisions on habitat quality. Moreover, environment and potential habitats constantly change, making habitat selection process heavily dependent on natural selection as individuals should consider ever occurring changes in predation, parasitism, intraspecific and interspecific competition levels, and resource availability. Therefore, it is often considered that environmental cues-based habitat selection should lead to source-sink population dynamics (*e.g.*, Hanski 1999).

1.2. Ecological traps

Animals normally prefer habitats of the highest quality over poor habitats. They are supposed to choose poor habitats only if better options are not temporarily available or do not exist at all (Ekman 1989). However, in rapidly changing ecosystems, especially affected by anthropogenic pressure (Hale & Swearer 2016; Robertson *et al.* 2013), the cues used to select proper habitats can be decoupled from the true quality of the habitat. This can lead to mistakes in habitat choice.

Because of rapid environmental changes affecting habitat structure, less preferred habitats may become equally or more attractive than the best habitats. In rapidly changing environments, animals may end up in the habitats that reduce their survival, reproduction, individual and inclusive fitness. These types of habitats have been referred to as ecological traps and sometimes also defined as evolutionary traps (Hale *et al*. 2015; Robertson & Hutto 2006; Robertson *et al*. 2013; Demeyrier *et al.* 2016). In terms of source-sink demographic dynamics, some most extreme ecological traps may transform into population sinks (Hanski 1999). Theory predicts that ecological traps and population sinks, where habitat quality is decoupled from the habitat's attractiveness, mostly occur in the environments affected by humans (Hale & Swearer 2016; Robertson *et al.* 2013).

In natural conditions, ecological traps often arise if one part of a habitat contains high numbers of more attractive cues suggesting a suitable place to live in or reproduce. It is suggested that decoupling habitat quality from its attractiveness happens under the following scenarios: (1) the intensity, expression and number of cues increase in a habitat which quality remains the same; (2) habitat quality and suitability significantly declines whereas the cues of habitat attractiveness remain the same in their expression and numbers (Robertson & Hutto 2006; Hale & Swearer 2016). Although characterization of ecological traps may look like an easy task, it is important to note that demonstrating an ecological trap in the wild is difficult. The first reason for this is that the cues involved in the preference and selection of the habitat must be identified with precision. Second, these cues are extremely difficult to manipulate experimentally following robust experimental designs (*e.g.*, Robertson & Hutto 2006). Experimental demonstration of an ecological trap in the wild is therefore limited despite the extensive efforts of empirical research to assess behavioural effects of traps (*e.g.*, Mänd *et al.* 2005; Robertson & Hutto 2006; Mägi *et al.* 2009; Hale & Swearer 2016). However, the decoupling habitat quality and its attractiveness can be experimentally done, especially in the decoupling scenarios where the cues of quality, the habitat attractiveness and its quality are easy to manipulate or detect.

1.3. Anthropogenic impact, human created cues, naturally occurring forest disturbances and ecological traps

Nowadays humans are the most important factor affecting forest ecosystems and biological diversity. Urbanization changes the environment of a growing number of animal species. It has been shown that anthropogenic changes are rapid, they involve larger aquatic and terrestrial areas worldwide, and only a few organisms can immediately follow changes caused by anthropogenic factors in their habitats. However, naturally occurring outbreaks of insects may also represent a major cause of habitat disturbances in the forest ecosystems (Barbosa *et al.* 2012; Moulinier *et al.* 2013), affecting communities of forest animals and plants and influencing their densities and organismal interactions (Vindstad *et al.* 2015). Anthropogenic landscapes are considered to be potential ecological traps for organisms, especially when artificial human-constructed cues match to ones that reflect true habitat quality in natural environments, being attractive but misleading signals in anthropogenic environment (Marzluff 2001; Robertson *et al.* 2013, Demeyrier *et al.* 2016). Humans often provide birds (Aves) with artificial nest boxes in populated areas, parklands, gardens and managed forests. For cavity nesting birds, such as the European pied flycatcher (*Ficedula hypoleuca* Pallas, 1764) and the great tit (*Parus major* Linnaeus, 1758), artificial nest boxes make every woodlot or parkland more attractive to settle than areas without artificial nest boxes. The presence of cavities and holes are among the most important cues for habitat selection in great tits and pied flycatchers (Hildén 1965). It has been shown that the density of nesting birds can be raised well above naturally occurring densities.

Birds are often used as a means of biological control to regulate pest outbreaks in forestry and agriculture practice (Duan *et al.* 2015). Biological control by provisioning nest boxes for insectivorous birds is a commonly used approach to attract hole-nesting birds, especially in Europe (Gosler 1993; Tilgar *et al.* 1999; Mols & Visser 2007; Mänd *et al.* 2005). Putting up nest boxes is a simple method to encourage avian populations at the sites of insect outbreaks (Jedlicka *et al.* 2011). Birds often prefer artificial nest boxes over natural holes, because artificial nest boxes are constructed to minimize nest predation, humid microclimate, nest soaking and improve nest illumination (Maziarz *et al.* 2016). Provisioning of nest boxes makes it easy to compensate for naturally low availability of cavities, which is a limiting factor in managed forests and populated areas. Importantly, some studies showed that great tits and pied flycatchers can be attracted to an area independent of the actual number of resources available in the habitat (Mänd *et al.* 2005; Kilgas *et al.* 2007).

Preference for a certain box design as reflected in its shape or size is species-specific and perhaps population-specific, or even a matter of individual choice (*e.g.*, Lambrechts *et al.* 2010). For instance, previous studies in secondary-cavity nesting great tits have shown that females prefer to breed in large nest boxes (Maziarz *et al.* 2016; Møller *et al.* 2014). In addition, clutch size has been shown to increase with the size of the nesting cavity, either through individual plastic adjustment or non-random distribution of individuals varying in reproductive capacity (Slagsvold 1987). Breeding in a large cavity might limit hyperthermia risks, reduce nestling competition for space or decrease predation risks inside the cavity, therefore not penalizing larger broods (Slagsvold 1987). This makes it possible to lure cavity-nesting birds to the areas with low levels of food available, thus, potentially causing ecological traps or sink habitats where individual fitness will decrease and mortality exceeds the birth rate (Gates & Gysel 1978; Kokko & Sutherland 2001; Schlaepfer *et al.* 2002). Moreover, insect outbreaks can deteriorate the environment themselves by defoliating local plants, reducing flowering and seed production, and diminishing the availability of arthropod (Arthropoda) food. The latter may cause hunger and death of nestlings in the nests of many insectivorous birds attracted by putting up artificial nest boxes. Thus, the activities to protect forests and agricultural land against pest insects by installing nest boxes to attract insectivorous birds may cause ecological traps for the birds lured to the area. It is important to note that the use of nest boxes and attraction of insectivorous birds to the forests, rural areas and cities has always been considered a “green” activity that improves environmental quality, protects nature and maintains populations of several bird species. This suggests that humans may possibly create ecological traps even during their environmental and nature protection activities, which needs more attention and research.

1.4. Blood parasites, water bodies and ecological traps

Landscape variables and ecological factors have often been used to understand and explain the spatial variation of the malaria disease in human populations (Kibret *et al.* 2017, 2019a, b; Endo & Eltahir 2018). These studies showed that the proximity to nearest water bodies, where parasite vectors reproduce, significantly affect the incidence of malaria risk across landscapes (Beck *et al.* 1994; Cano *et al.* 2006; Endo *et al.* 2015). It was found that malaria prevalence in households within 160 m from nearest water body in Senegal was 74 %, while the prevalence at 900 m from the marsh was around 17 % (Trape *et al.* 1992). Similar results were obtained also in other human studies (Jobin 1999; Endo & Eltahir 2018; Kibret *et al.* 2019a, b).

In non-human animals, parasitism is considered to be one of the strongest forces shaping the community structure of host species through the effects on trophic interactions, food webs, competitive interactions and biodiversity (Svensson-Coelho & Ricklefs 2011; Schmid-Hempel 2011).

Haemosporidians (Haemosporida) are obligate parasites that infect a wide range of vertebrates and use dipteran insects as vectors (Valkiūnas 2004). Infections of avian hosts with blood parasites belonging to the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* may have detrimental effects on host reproductive success and survival probability (Valkiūnas 1998; Merino *et al.* 2000; Valkiūnas & Iezhova 2004; Valkiūnas 2004; Palinauskas *et al.* 2009; Martínez-de la Puente *et al.* 2010; Krams *et al.* 2013; de Jong *et al.* 2014). Parasite prevalence and infection intensity (parasitemia) often depend on the host immune system and the outcome of an arms race between host immunity and the ability of parasites to invade their hosts (*e.g.*, Krams *et al.* 2012a). However, vector prevalence and distribution may also have significant effects on an individual's risk of infection (*e.g.*, Allander & Bennett 1994; Zhou *et al.* 2012; Krams *et al.* 2010, 2013; Martínez-De la Puente *et al.* 2010; Loiseau *et al.* 2012).

It has been found that avian haemosporidian parasites are not homogeneously distributed across their hosts' habitats and populations (Lacorte *et al.* 2013). Blood parasites are often absent in the blood of birds in marine, saline, arid or alpine/high altitude environments, which can be explained by the absence or scarcity of parasite vectors (Bennett *et al.* 1992; Rytkönen *et al.* 1996; Piersma 1997; Figuerola 1999; Sol *et al.* 2000; Atkinson *et al.* 2005; Hellgren *et al.* 2008; Krams *et al.* 2012a; Martínez-De la Puente *et al.* 2013). At high latitudes, the period of active transmission of blood parasites occurs during the summer season (van Riper 1991; Atkinson *et al.* 1988), while at low latitudes, it is associated with the rainy season (Young *et al.* 1993). Thus, proliferation of vector-borne parasitic diseases is linked not only to the immunity of hosts, but also to various aspects of their ecology, such as the availability of suitable habitats for the vectors (*e.g.*, Arriero *et al.* 2008; Arriero 2009; Sehgal 2010).

However, relatively little is known about the habitat preferences of the dipteran vectors that transmit avian blood parasites. It is certain that mosquitoes (*Culicidae*) require standing water to reproduce, which increases the probability of *Plasmodium* infections in the vicinity of lakes and ponds (Kettle 1995; Ishtiaq *et al.* 2008; Njabo *et al.* 2009; Krams *et al.* 2010, 2012a, b), and slow rivers (Wood *et al.* 2007). Biting midges (*Ceratopogonidae*) are found in fens, bogs, marshes, compost, mud and stream margins (Hendry 1989). Blackflies (*Simuliidae*) are found wherever there is permanent or semi-permanent running water, which is required for development during larval and pupal stages. Thus, the majority of vectors of bird blood parasites require wetlands to reproduce. Although this may increase the prevalence of blood parasites in some birds living near lakes, streams and bogs (*e.g.*, Wood *et al.* 2007; Krams *et al.* 2010), the associations between parasite prevalence and habitat type of their hosts are not yet well understood. Moreover, a negative relationship between the distance from water bodies and the intensity and prevalence of avian haemosporidian infections might suggest ecological traps for the birds that attempt to breed in the vicinity of water bodies.

1.5. Aims of the thesis

The main aim of the thesis is to test whether ecological traps of bird populations are more widespread than previously considered and whether these traps can arise, because of nature protection-related activities by humans, and whether the areas around forest lakes and streams, beautiful land with a high biodiversity level, can decrease offspring survival of breeding birds.

Putting up nest boxes in the forest patches affected by insect outbreaks may attract cavity-nesting birds to ecological traps. The first goal of this thesis (**I**) was to test whether great tits breeding in Scots pine (*Pinus sylvestris* Linnaeus 1753) forests heavily damaged by outbreaking of the great web-spinning pine-sawfly (*Acantholyda posticalis* Matsumura, 1912) suffer fitness costs. Although insect larvae are the preferred food for great tit nestlings and fledglings (Rytkönen & Krams 2003), the sawfly is a defoliator pest, which during its outbreaks decreases the number and biomass of other insects. Therefore, we predicted (1) similar clutch sizes between the patches damaged by web-spinning sawflies and healthy patches. We expected (2) smaller fledgling numbers, lower fledgling body mass and shorter tarsus lengths due to malnutrition in the nest boxes located in the patches damaged by sawflies. Since total larval biomass (sawfly and other insect larval biomass) can be expected to be related to the amount of available foliage, we used estimates of live tree crown volume and canopy cover as indirect measures of larval biomass (Brūmelis *et al.* 2020). We expected lower larval biomass in the areas affected by great web-spinning sawflies (**I**).

Some previous studies done on humans and other animals showed that blood parasite burden and their detrimental effect may increase near water bodies. The second goal of this thesis (**II**) was to test whether there is a positive association between proximity to the nearest wetlands and parasite prevalence in the breeding pied flycatcher, and whether forest stands located further away from forest lakes and streams can be considered parasite-free areas. To find out the effects caused by the proximity of forest water bodies, we performed a study 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 (**II**).

Most studies of bird blood parasites have been conducted during the reproductive season of birds, when parasite vectors are predicted to be most abundant. However, some studies have also demonstrated high parasite prevalence outside the breeding season and even during the winter (Hauptmanová *et al.* 2002; Dunn *et al.* 2013, 2014), showing that birds may be at risk of infection in late summer and early autumn, while parasite vectors remain active (*e.g.*, Cheke *et al.* 1976; Rintamäki *et al.* 1999; Ishak *et al.* 2010; Kimura *et al.* 2010). The effects of blood parasite infections on their hosts outside the breeding season, however, have not yet been tested. The third goal of this thesis (**III**) was to investigate whether prevalence and infection intensity of blood parasites are related to the distance of territories of wintering mixed-species tit (*Paridae*) groups, consisting of willow tits (*Poecile montanus* Conrad von Baldenstein, 1827) and crested tits (*Lophophanes cristatus* Linnaeus, 1758), from forest lakes, streams and bogs where parasite vectors reproduce. We predicted a negative correlation between prevalence and intensity of infection and the distance of bird territories from water bodies, as it is reported in human malaria (Midega *et al.* 2012) (**III**). We also checked whether haemosporidian infections of parids increase their probability of being predated upon by the pygmy owl (*Glaucidium passerinum* Linnaeus, 1758), the principal predator of passerine (Passeriformes) birds in northern Europe (Kullberg 1995; Kullberg & Ekman 2000) (**III**).

2. MATERIALS AND METHODS

2.1. Study sites and bird species (I, II, III)

The breeding ecology of great tits was investigated near Daugavpils, south-eastern Latvia (55.55° N, 26.34° E), where the study area covers young Scots pine stands affected by an on-going mass outbreak of the great web-spinning pine-sawfly (**I**).

The second (**II**) and third (**III**) study was conducted in the vicinity of Krāslava in south-eastern Latvia (56° N, 27° E). The study area covers coniferous (Pinopsida) and mixed forest plantations dominated by Scots pines (Rytkönen & Krams 2003). The second study (**II**) 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. The diverse system of forest water bodies provided suitable habitats for reproduction of all kinds of blood parasite vectors (**III**). Notably, the major part of the study area located away from forest water bodies (**II**) was covered by a markedly homogeneous coniferous habitat dominated by Scots pine, while forests near water bodies contained much higher tree species biodiversity consisting of Scots pine, grey alder (*Alnus incana* Moench, 1794), black alder (*Alnus glutinosa* Gaertner, 1791), Norway spruce (*Picea abies* Karsten, 1881), silver birch (*Betula pendula* Roth, 1788), bird cherry (*Prunus padus* Linnaeus, 1753), European hazel (*Corylus avellana* Karsten, 1881), English oak (*Quercus robur* Linnaeus, 1753) and common juniper (*Juniperus communis* Linnaeus, 1753) (Rytkönen & Krams 2003; Brūmelis *et al.* 2020). 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 the majority of water bodies in the Joint Stock Company (JSC) “Latvia’s State Forests” managed pine stands and private forests. The third study (**III**) was done at the same area, but it covered a larger territory (c. 10 km^2) containing forest lakes, bogs, small streams and one large river with a number of bays suitable for mosquito reproduction. As in study **II**, the majority of the area was dry pine forest on sandy soil with nearly no understory and did not contain any ditches or temporary water pools.

The studies **I** and **II** were carried out during the reproductive season of great tits and pied flycatchers, while the study **III** was performed outside the breeding season of willow tits and crested tits.

Pied flycatchers are small (10-18 g) insectivorous cavity-nesting passerine birds (Lundberg & Alatalo 1992). This species reproduces in Europe and spends the winter season in western Africa. Pied flycatchers are among the most common bird species in Europe during the summer season, which prefers to nest in artificial nest boxes. By installing nest boxes, this bird can be attracted to almost any type of woods, parks, gardens.

Great tits are small passerine birds that belong to the family *Paridae*. These birds are common and widespread throughout Europe, Central and Northern Asia, the Middle East and North Africa. They live in any kind of woodland, parkland and are common in populated areas. Great tits live in Latvia throughout the year. This species occupies natural cavities and artificial nest boxes. Great tits are mostly insectivorous in summer, while they can eat any kind of food outside the breeding season and especially in winter. The population of pied flycatchers and great tits at Krāslava has been studied as part of a long-term project of the ecology of cavity-nesting birds carried out since the mid-1980s (Rytkönen & Krams 2003; Ruuskanen *et al.* 2011; Samplonius *et al.* 2018). The pied flycatcher and the great tit are one of the most intensely studied bird species in the world.

2.2. Outbreak of the great web-spinning pine-sawfly (I)

The outbreak of the great web-spinning pine-sawfly was last observed in summer 2013. This is the second observed outbreak of this pest in Latvia. The previous outbreak was observed some 40 km eastwards during 1966–1982. Prolonged outbreaks are typical for great web-spinning sawflies. Years of intensive flight are followed by years when the majority of larvae fall in diapause. Consequently, years with heavy tree defoliation are followed by years when trees are able to partly recover their foliage. This study was conducted in 2019 when flight activity was low and the larvae of great web-spinning sawflies were hardly available as a food resource for birds in the spring–summer period.

Great web-spinning sawfly adults emerge from the soil and females lay eggs on needles of Scots pine in June (Voolma *et al.* 2016). Sawfly larvae consume the needles of pines and feed on the needle substrate until the beginning of August. At the fourth larval instar stage the larvae move to the soil where they stay for two to five years before they emerge after a short (8 – 10 days) pupation (Ghimire *et al.* 2013). The highly variable larval stage makes outbreaks of great web-spinning sawflies unpredictable (Ghimire *et al.* 2013). Importantly, patches damaged by a web-spinning sawfly outbreak are easy to distinguish from healthy patches, because in the damaged areas pines are strikingly defoliated (Brūmelis *et al.* 2020).

2.3. Nest box arrangement to study effects caused by phytophagous great web-spinning pine-sawfly (I)

Breeding success, fledgling number, fledgling body mass and tarsus length of great tit nestlings were recorded in two contrasting types of forest patches - the pine forest damaged by web-spinning sawflies and a nearby healthy pine forest. We chose six areas in the affected pine forest and five areas in the nearby healthy forest. We put up 12 nest boxes in each of these patches (72 nest boxes in the affected forest and 60 nest boxes in the healthy forest). Out of 132 nest boxes, great tits occupied 34 nest boxes in the damaged forest and 31 nest boxes in the healthy forest (65 nest boxes in total). Great tit offspring successfully fledged in 59 nest boxes (30 nest boxes in the damaged areas and 29 nest boxes in the healthy areas). The total area of the damaged forest was c. 120 ha. The total size of studied patches with nest boxes was c. 3.8 ha. The distance between study patches (each containing 12 nest boxes) was at least 480 m. To avoid competition, the distance between neighbouring boxes was c. 50 m in each of the 11 study patches. The nest boxes were checked regularly to record basic breeding parameters, such as the number of eggs and the number of fledglings, which is an indication of breeding success. To assess offspring quality, all nestlings were weighed with a Pesola spring balance to a precision of 0.1 g and their tarsi were measured with sliding callipers to the nearest 0.1 mm on day 15 post hatch. The internal size of the nest boxes was 0.13 × 0.13 × 0.25 m and the diameter of the entrance was 0.036 m.

2.4. Food resources of breeding birds (I)

We estimated the amount of food resources available in each forest patch by using the frassfall method (Rytkönen & Krams 2003). Frass production by larvae was measured using plastic funnels (diameter 35 cm) with a paper coffee filter (size 1 × 4) attached to each funnel. The filter lets rainwater go through, but frass produced by herbivory larvae is retained inside the filter. We used three funnels in each study patch ($n = 33$). The funnels were attached to trunks of randomly chosen pines, and the distance between the funnels was c. 60 m. As soon as the first nestlings in the patch reached the age of 7 days, the funnels were placed for a period of 4 days. The filters with the frass were preserved in a freezer. The frass production was determined by counting the frass items in each filter, and the average diameter of the frass items was determined by measuring randomly sampled frass items in each filter with an ocular micrometre. We estimated larval biomass from frass dry mass by using an allometric relationship between frass diameter and frass dry mass (Rytkönen & Orell 2001), and the equation by Tinbergen and Dietz (1994). As we could not discriminate between frass produced by larvae of other insects - autumnal moths (*Epirrita autumnata* Borkhausen, 1794) and sawflies (Zandt 1994), this research provided an estimation of the total food resources available in each forest patch.

2.5. Tree canopy in the patches of sawfly outbreak and in the unaffected patches (I)

We studied how the condition of forest patches affects breeding parameters of great tits. We distinguished between healthy (< 25 % foliage loss), damaged (25–75 % foliage loss) and dead trees (< 25 % foliage remaining) (Brūmelis *et al.* 2020). We measured the following three condition parameters: (1) total canopy cover of pines (%), (2) the relative number of dead and dying trees with 75–100 % loss of needles due to web-spinning sawfly damage (%) and (3) the total tree crown volume (m^3 ha^{-1}). The relative number (%) of dead trees reflects the rate of damage done by a pest. High amounts of leaf (needle) damage eventually led to the death of a tree. The total volume of tree crowns in the patch is important, because it reflects the total amount of substrate that insectivorous birds can use to collect their food.

In each plot, diameter (DBH - diameter at breast height) of all trees at a height of 1.3 m was measured. In addition, measurement of tree crown parameters (height to top and base of the live tree crown, and width of the tree crown in two perpendicular directions) were made in each plot for 2 – 4 trees with different size and extent of damage. A Haglof VL5 vertex was used to measure height to top and base (lowest living branch) of the live tree crown. The GRS densitometer was used to precisely locate the edge of the crown for width measurements. Tree crown measurements were made for 76 healthy and 16 damaged (more than 25 % of needles lost) pine trees. Tree crown volume was estimated as an ellipsoid, as suggested for practical purposes for Scots pine (Rautiainen *et al.* 2008). The allometric relationship between stem diameter and crown volume for sampled trees for crown parameters was used to estimate volume for all trees in plots using an exponential regression model, separately for healthy [volume = 10.529588 * EXP (0.068715 * DBH)] and damaged [volume = 3.85498*EXP (0.09189*DBH)] trees. The exponential model was found to best explain the relationship between DBH and crown volume ($R^2 = 0.525$ and $R^2 = 0.605$ for healthy and damaged trees, respectively), and was superior or similar to a linear and power relationship, respectively. For the calculations, we also included data from 82 pine trees measured in this study area (Brūmelis *et al.* 2020). The total tree crown volume per hectare in the stands was then estimated.

2.6. Nest box arrangement to study bird blood parasite abundance in relation to the distance to forest water bodies in the breeding season (II)

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, 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 the European pine marten (*Martes martes* Linnaeus, 1758) or other predators, and none were deserted due to our study 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 (Ojanen 1987; Lundberg & Alatalo 1992).

2.7. Investigation of blood parasites in the blood of members of mixed-species tit groups in relation to the distance to nearest forest water bodies during wintering season (III)

The data were obtained from 20 mixed-species flocks containing 4–5 crested tits (mean number of individuals 4.30 ± 0.44, mean ± standard deviation (SD); 86 individuals in total) and 4–6 willow tits (mean number of individuals 4.10 ± 0.49, mean ± SD; 82 individuals in total). The birds were trapped by mist nets at temporary feeders baited with sunflower seeds. All flock members were captured in September. Willow tits and crested tits were sexed and aged (as adult or juvenile). The shape of the rectrices of willow and crested tits (Laaksonen & Lehikoinen 1976), and the colour of the iris of crested tits (Bardin 1979; Lens & Dhondt 1992) were used to determine age. Sexual dimorphism in wing and tarsus length were used to sex individuals (Koivula & Orell 1988). Each bird was banded with metal and individual plastic bands. Each mixed-species flock was followed for 18–24 h within 5–6 days to detect its boundaries using a Magellan GPS receiver (MiTAC Digital Corporation, Santa Clara, CA, USA). An observer recorded the flock's coordinates every five minutes, while following adult willow and crested tits. We determined the distance between the flock and the nearest water-body as the distance between the edge of the bog (all of the lakes were surrounded by bogs), stream or river, and the closest point of the territory to the water-body visited by flock members. The distances were measured on a digital map.

2.8. Bird survival in winter in relation to their infection status (III)

We estimated the winter survival of birds in the beginning of February. The birds that disappeared from the flocks, but were found again as members of adjacent flocks or as breeding birds in spring, were included in the analysis as survivors. We estimated the predation rate of willow tits and crested tits by counting the number of individuals in food caches of pygmy owls, while checking nest boxes between October and January. We assume that all other birds not found were dead.

2.9. Blood parasite detection and identification (II, III)

At capture, blood samples (150 μL) were taken from the tarsal vein. For identification of blood parasites and leucocytes, a drop of blood was smeared on two to three individually marked microscope slides, air-dried, fixed in absolute methanol (CH_3OH) and stained with Giemsa stain (Bennett 1970; Valkiūnas 2004). Smears were screened with a light microscope under oil immersion at 1,000× magnification for *Haemoproteus* and *Plasmodium*, and at 500× magnification for *Leucocytozoon*, *Trypanosoma* and *Microfilaria* detection. 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*. Individuals were classified as infected when smears were positive for at least one haemoparasite taxon. The intensity of infection was estimated as the number of parasite gametocytes per 10,000 erythrocytes (Valkiūnas 2004).

2.10. Estimation of blood parasite vector numbers in the nest boxes of pied flycatchers (II)

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 three and six 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 × 14 cm) of thick paper covered by a layer of non-hardening epoxide resin (Krams *et al.* 2013). 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 (mesh size 1 × 1 cm) 1 cm above the trap, 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.

3. RESULTS

3.1. Larval biomass in damaged and healthy forest patches (I)

The overall biomass of canopy-dwelling insect larvae during the nestling period of great tits was significantly negatively associated with sawfly damage. Larval biomass in the canopy increased from the damaged forest patches to the healthy forest patches: the biomass was higher in patches with greater canopy volume ($r_s = 0.882$, $P = 0.001$; Fig. 1A), it increased in patches with greater total pine canopy cover ($r_s = 0.945$, $P < 0.001$; Fig. 1B), while the biomass decreased in patches with a high number of dead trees ($r_s = -0.934$, $P < 0.001$; Fig. 1C).

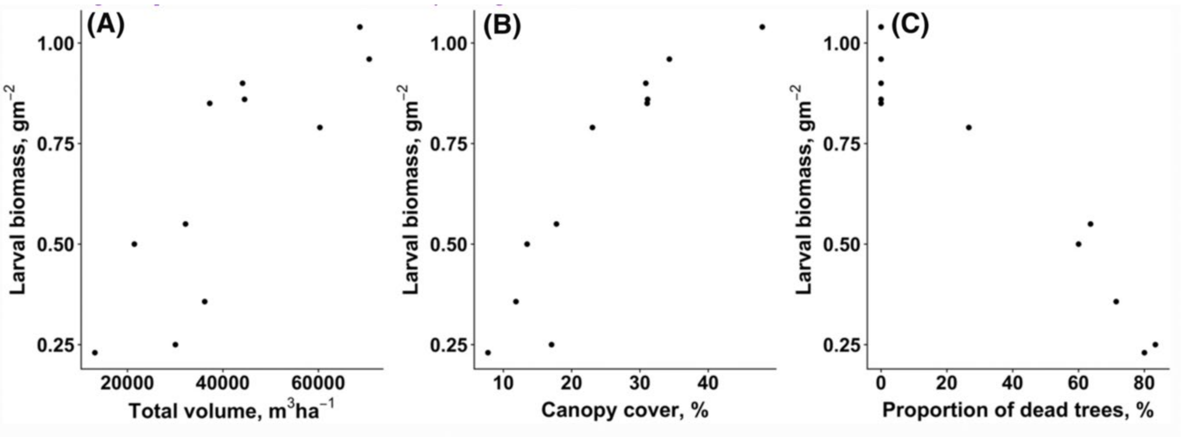

Figure 1. Correlations between larval biomass and total canopy volume (A), total pine canopy cover (B), and rate of dead trees (C).

3.2. Fitness parameters: clutch size, number of clutches, fledgling number, fledgling size and body mass (I)

Clutch size did not depend on the total pine canopy cover (slope estimate: -0.0001, 95 % credibility interval (CI): (-0.007, 0.007), $P = 1.00$, Fig. 2A), the proportion of dead trees (estimate: -0.000, CI: (-0.002, 0.002), $P = 0.984$, Fig. 2B), nor on total canopy volume (estimate: -0.004, CI: (-0.087, 0.078), $P = 0.992$, Fig. 2C). We did not observe second clutches of great tits in the forest damaged by the outbreak of great web-spinning sawflies, while 58.6 % ($n = 17$) of the great tits had second clutches in the forest unaffected by the pest.

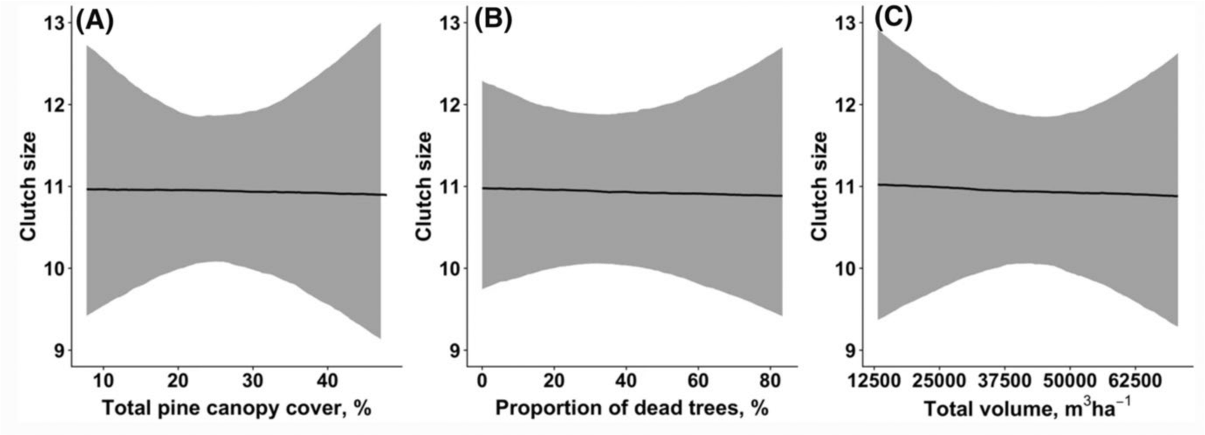

Figure 2. Associations between the clutch size of great tits and total pine canopy cover (A), rate of dead trees (B), total canopy volume (C). Solid lines show the estimated trend lines by the model and grey-shaded areas represent 95 % credibility intervals.

The number of fledglings increased with the total pine canopy cover (estimate: 0.099, CI: (0.062, 0.135), *P* < 0.001, Fig. 3A), decreased with the number of dead trees (estimate: -0.033, CI: (-0.040, -0.027), *P* < 0.001, Fig. 3B) and increased with total canopy volume (estimate: 0.973, CI: (0.371, 1.565), *P* = 0.016, Fig. 3C).

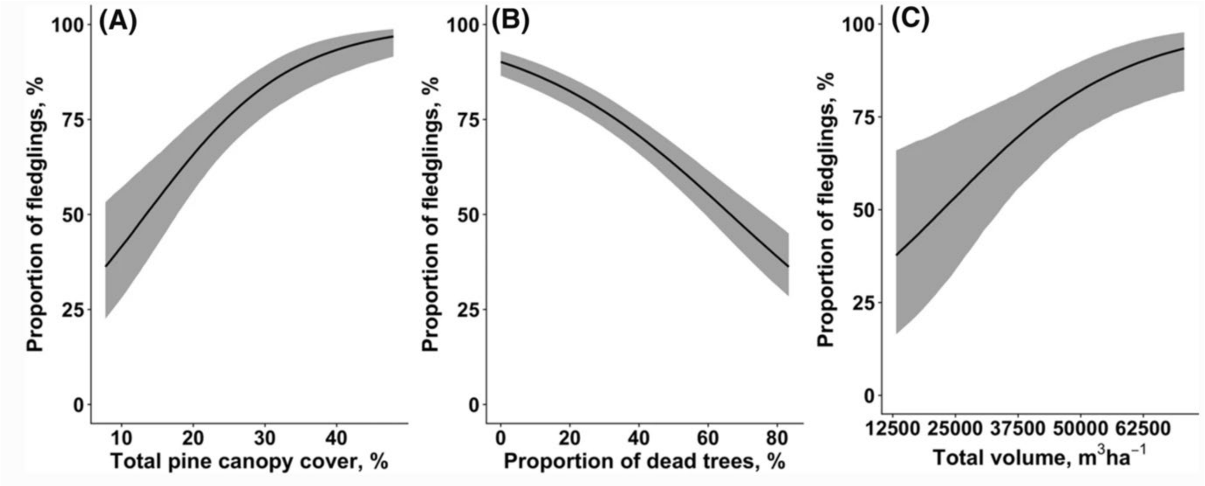

Figure 3. Associations between the proportion of fledglings per clutch and total pine canopy cover (A), rate of dead trees (B) and total canopy volume (C).

Great web-spinning sawfly outbreak negatively affected the size of fledglings. Tarsus length of fledglings increased with the total pine canopy cover (estimate: 0.011, CI: (0.001, 0.020), *P* = 0.071, Fig. 4A), declined with increased number of dead trees (estimate: -0.004, CI: (-0.007, -0.001), *P* = 0.061, Fig. 4B) and increased with total canopy volume (estimate: 0.110, CI: (0.000, 0.222), *P* = 0.128, Fig. 4C).

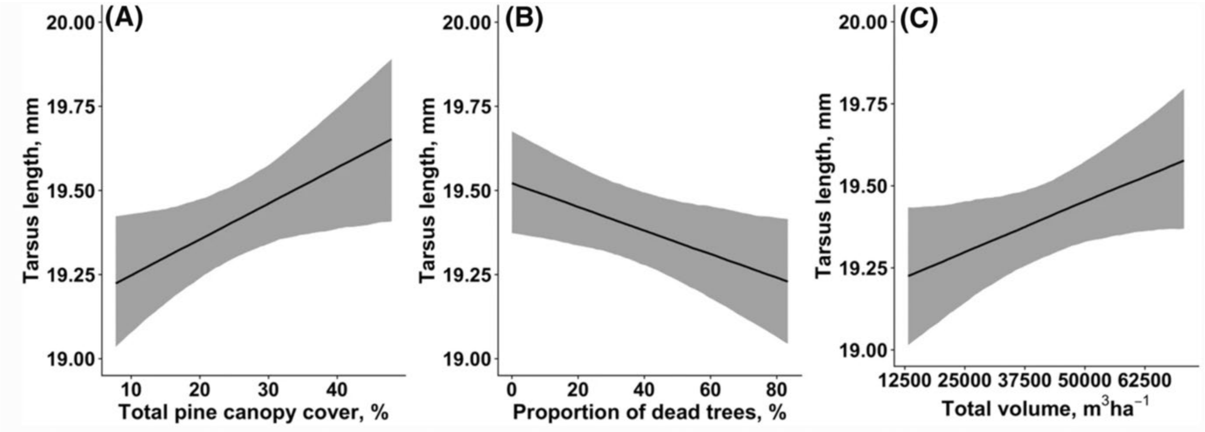

Figure 4. Associations between fledgling tarsus length and total pine canopy cover (A), rate of dead trees (B) and total canopy volume (C).

Body mass of fledglings increased with the total pine canopy cover (estimate: 0.033, CI: (0.017, 0.048), *P* < 0.001, Fig. 5A), declined with increasing number of dead trees (estimate: -0.012, CI: (-0.014, -0.010), *P* < 0.001, Fig. 5B) and non-significantly increased with the total canopy volume (estimate: 0.289, CI: (0.006, 0.567), *P* = 0.084, Fig. 5C).

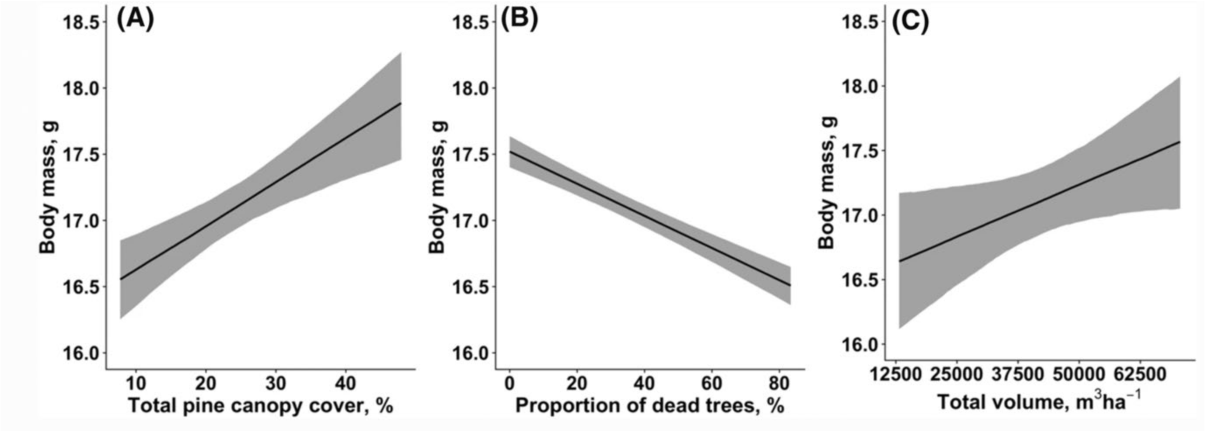

Figure 5. Associations between fledgling body mass and total pine canopy cover (A), rate of dead trees (B) and total canopy volume (C).

3.3. Parasite abundance (prevalence, parasitemia) in relation to the distance to forest water bodies in breeding pied flycatchers (II)

Haemoproteus

Significant differences in *Haemoproteus* prevalence between sexes and within each sex at the beginning of the breeding season, the end of the season or across the season were not found (Fig. 6A). *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, CI: (-11.71, -0.03); Fig. 6A), suggesting a rise in *Haemoproteus* prevalence in males from the beginning to the end of the breeding season. Importantly, *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); Fig. 6B), but had no significant effect at the beginning of the season (estimate: -3.23, CI: (-7.59, 0.15); Fig. 6B). Distance and sex interaction had no significant effect on *Haemoproteus* prevalence (estimate: 3.33, CI: (-1.35, 8.45)).

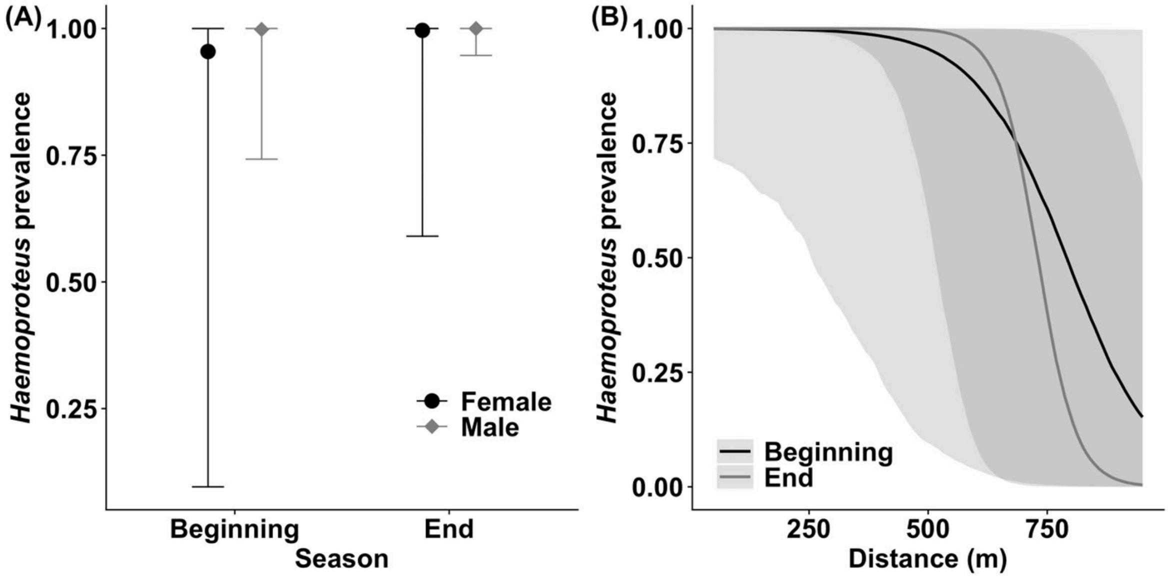

Figure 6. (A) *Haemoproteus* prevalence in the blood of male and female pied flycatchers at the beginning and the end of the breeding season. Error bars represent 95 % credibility intervals. (B) The association between the distance from the nearest water bodies and *Haemoproteus* prevalence at the beginning and end of the breeding season. Solid lines show the estimated trend lines 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), Fig. 7A). *Haemoproteus* parasitemia significantly increased during the breeding season in both sexes (estimates from -2.686 to -0.918; Fig. 7A). 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); Fig. 7B).

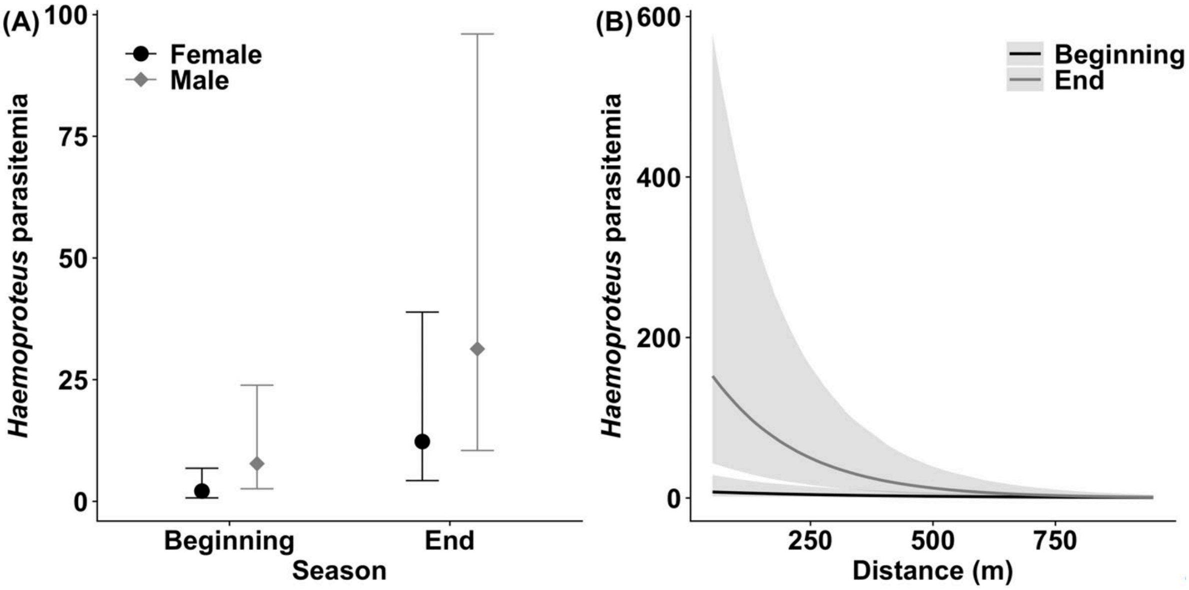

Figure 7. *Haemoproteus* parasitemia in male and female pied flycatchers at the beginning and the end of the breeding season. Error bars represent 95 % credibility intervals. (B) The relationship between the *Haemoproteus* parasitemia and the distance to the nearest water bodies at the beginning and the end of the breeding season. Solid lines show the estimated trend lines by the model and grey-shaded areas represent 95 % credibility intervals.

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); Fig. 8A) and male flycatchers (estimate: -5.96, CI: (-13.08, -1.61); Fig. 8A). 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 (Fig. 8B). 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)).

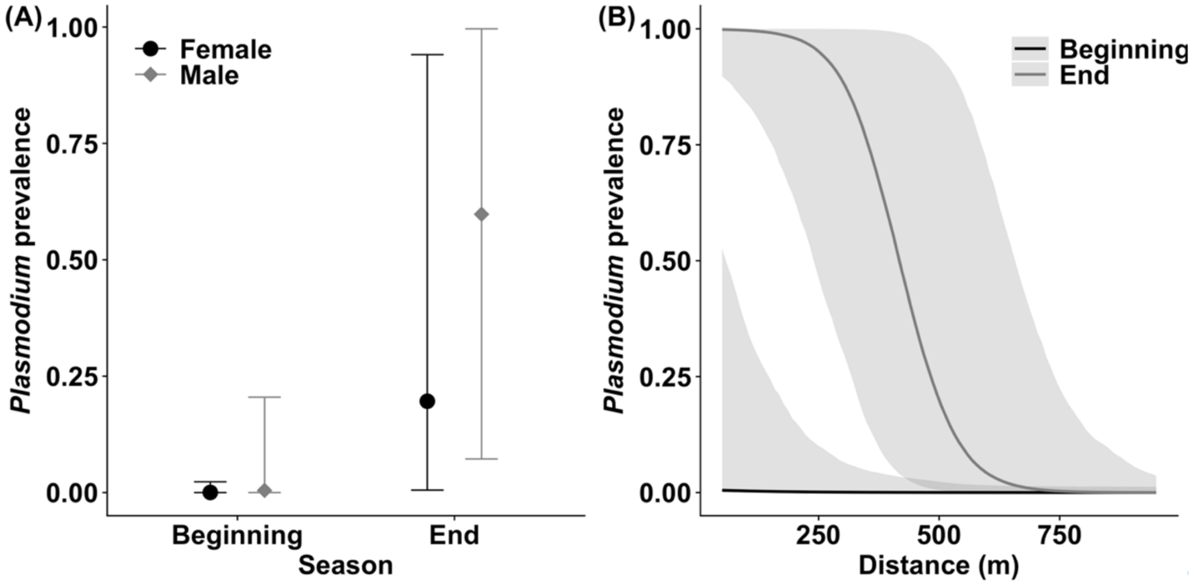

Figure 8. (A) *Plasmodium* prevalence in the blood of male and female pied flycatchers at the beginning and the end of the breeding season. Error bars represent 95 % credibility intervals. (B) The relationship between the distance from the nearest water bodies and *Plasmodium* prevalence at the beginning and end of the breeding season. Solid lines show the estimated trend lines 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 (estimate: -2.85, CI: (-4.14, -1.72); Fig. 9A). *Plasmodium* parasitemia was not related to the distance to the nearest water body (estimate: 1.51, CI: (-3.27, 0.07); Fig. 9B), 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)).

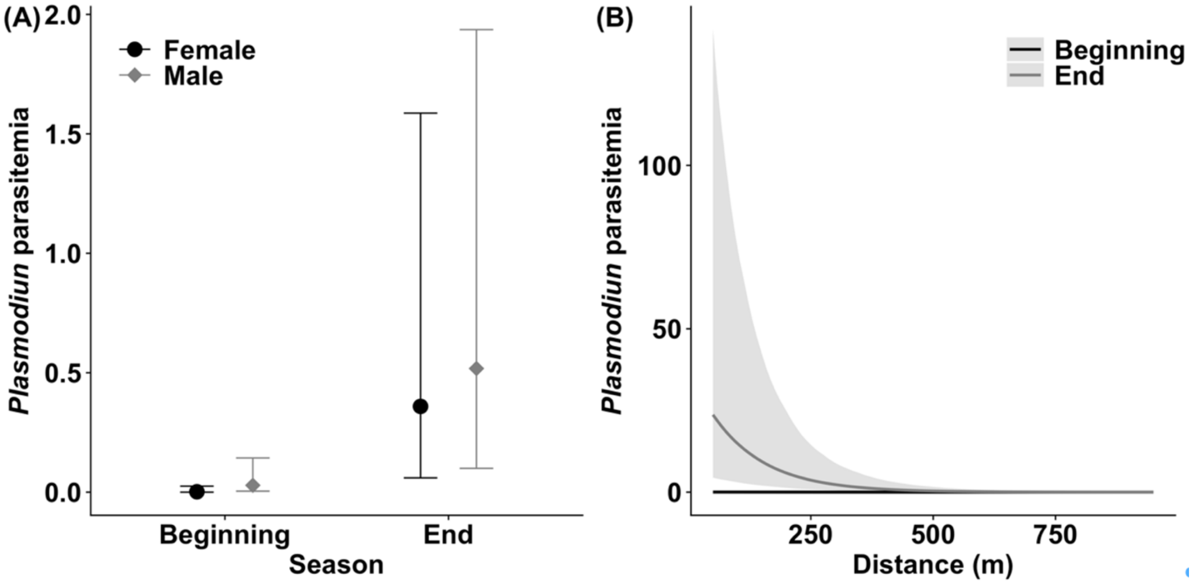

Figure 9. (A) *Plasmodium* parasitemia in male and female pied flycatchers at the beginning and end of the breeding season. Error bars represent 95 % credibility intervals. (B) The relationship between *Plasmodium* parasitemia and the distance to the nearest water bodies at the beginning and end of the breeding season. Solid lines show the estimated trend lines by the model and grey-shaded areas represent 95 % credibility intervals.

3.4. Parasite vector abundance (II)

In total, during 7 days, we trapped 1130 blood-sucking insects (524 biting midges, 575 mosquitoes and 31 blackflies) that entered 32 nest boxes inhabited by pied flycatchers. We found a significant negative correlation between the number of parasite vectors and the distance to the nearest water body (Spearman's $r = -0.886$, $n = 32$, $P < 0.0001$, Fig. 10).

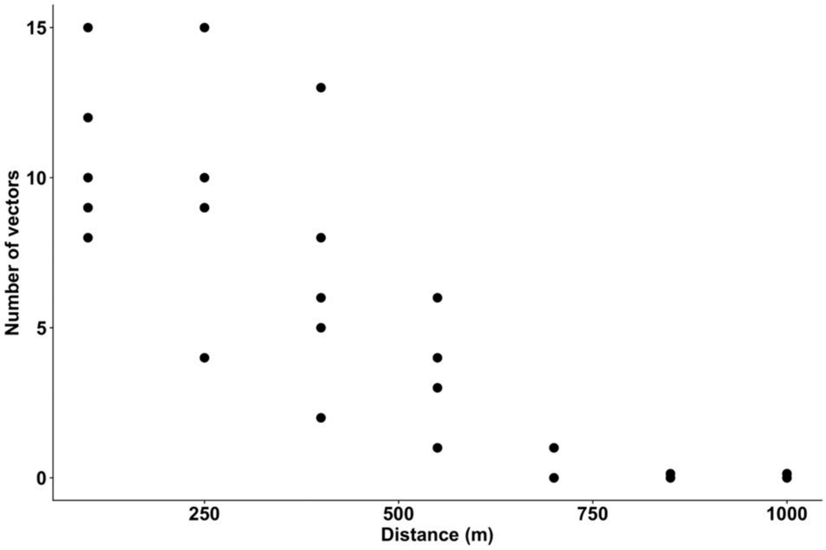

Figure 10. The relationship between the distance to the nearest forest water body and the number of parasite vectors trapped in nest boxes of pied flycatchers.

3.5. Fitness parameters of pied flycatchers (II)

The distance to the nearest water body did not affect clutch size (estimate: 0.02, CI: (-0.09, 0.12), Fig. 11A), while the distance had a positive effect on the fledgling number (estimate: 0.13, CI: (0.02, 0.25), Fig. 11B). Non-linear effects were observed for the distance to the nearest water body on fledgling body mass (estimate: 7.21, CI: (3.76, 12.39), Fig. 11C) and fledgling tarsus length (estimate: 0.22, CI: (0.07, 0.55), Fig. 11D), but non-significant effect 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 (0.21, 0.32)).

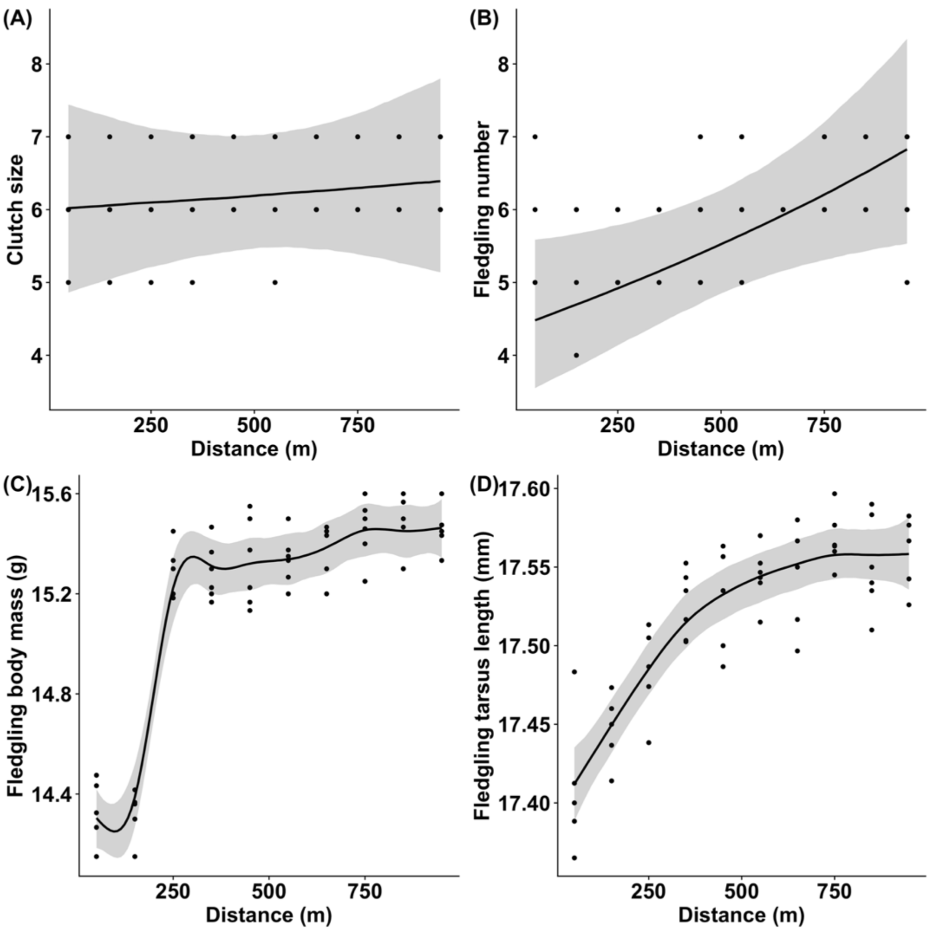

Figure 11. The relationships between the distance to the nearest forest water bodies and clutch size (A), fledgling number (B), fledgling body mass (C) and fledgling tarsus length of pied flycatchers (D). Solid lines show the estimated trend lines by the model and grey-shaded areas represent 95 % credibility intervals.

3.6. Parasite prevalence and parasitemia in members of wintering mixed-species groups of willow tits and crested tits (III)

Crested tits were infected only by *Haemoproteus majoris* (Laveran, 1902), while willow tits were infected with *Haemoproteus majoris* and *Plasmodium circumflexum* (Kikuth, 1931). *Leucocytozoon*, *Trypanosoma* and Microfilaria parasites were not found. The parasitemias of crested tits infected by *Haemoproteus* (1.57 ± 4.24 gametocytes/10,000 erythrocytes) and willow tits infected by *Haemoproteus* (1.19 ± 2.80 gametocytes/10,000 erythrocytes), and *Plasmodium* (0.35 ± 0.72 gametocytes/10,000 erythrocytes) were identified as being low. Both bird species did not differ statistically in *Haemoproteus* parasitemias (one-way ANOVA, $F_{1,162} = 0.47$, $P = 0.50$). In crested tits, *Haemoproteus* parasitemia did not vary significantly with distance from water bodies (one-way ANOVA, $F_{19,66} = 0.88$, $P = 0.61$). In willow tits, we also did not find any significant variation of *Haemoproteus* parasitemia (one-way ANOVA, $F_{19,63}$ = 1.23, P = 0.27), while we found a significant variation in *Plasmodium* parasitemia (one-way ANOVA, $F_{19,63}$ = 4.07, $P < 0.0001$) with distance from water bodies.

Prevalence of infected individuals with *Haemoproteus* within each bird group in crested tits varied from 0 to 50 % (18.75 ± 19.25 %) and from 0 to 100 % in willow tits (32.50 ± 38.41 %). The prevalence of *Haemoproteus* significantly differed between crested tits (15 infected and 71 non-infected, prevalence 17.44 %) and willow tits (26 infected and 56 non-infected, prevalence 31.71 %; Fisher's exact test, $P = 0.047$). The proportion of individuals infected with *Plasmodium* varied between 0 and 100 % (23.75 ± 35.80 %) in willow tit flocks. *Plasmodium* prevalence of willow tits (19 infected and 63 non-infected, prevalence 23.17 %) and crested tits (all 86 non-infected and 0 infected, prevalence 0 %) differed significantly as no *Plasmodium* infection was detected in crested tits (Fisher's exact test, $P = 0$). *Haemoproteus* and *Plasmodium* prevalence did not differ between adult (13 infected and 27 non-infected) and young willow tits (13 infected and 29 noninfected; Fisher's exact test, $P = 1$). Fifteen willow tits had mixed infections of *Haemoproteus* and *Plasmodium*.

Binary logistic regression (Nagelkerke's $R^2 = 0.272$, $P = 0.001$) revealed that proximity to water bodies increased the prevalence of *Haemoproteus* in crested tits ($b = -0.005$, $P = 0.002$, Fig. 12), while age ($b = 0.27$, $P = 0.62$), sex ($b = -0.48$, $P = 0.39$), tarsus length ($b = 0.07$, $P = 0.67$), wing length ($b = 0.052$, $P = 0.71$) and body mass ($b = 0.09$, $P = 0.49$) did not affect the prevalence of *Haemoproteus*.

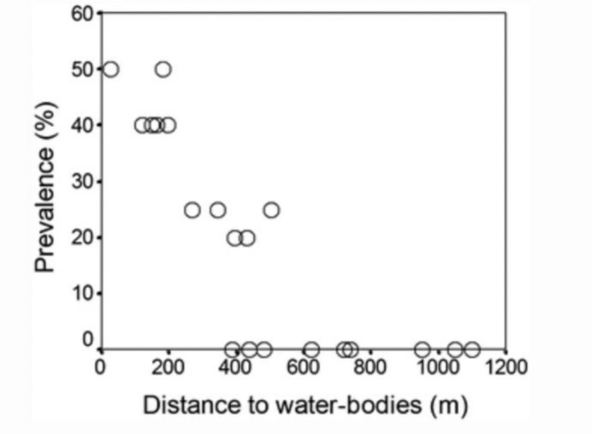

Figure 12. Relationship between distance to the nearest water bodies and prevalence of *Haemoproteus* in crested tits.

Binary logistic regression analysis (Nagelkerke's $R^2 = 0.543$, $P < 0.001$) showed that distance to water bodies was inversely related to *Haemoproteus* prevalence in flocks of willow tits ($b =$

-0.009, $P < 0.0001$, Fig. 13), while age ($b = 0.22$, $P = 0.64$), sex ($b = 0.30$, $P = 0.53$), tarsus length ($b = 0.01$, $P = 0.69$), wing length ($b = 0.093$, $P = 0.44$) and body mass ($b = 0.50$, $P = 0.35$) did not affect parasite infection.

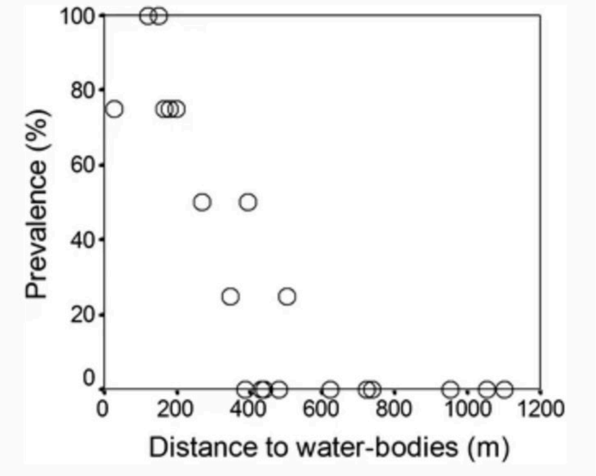

Figure 13. Relationship between distance to the nearest water bodies and prevalence of *Haemoproteus* in willow tits.

Proximity to forest lakes increased the risk of *Plasmodium* infection in willow tits ($b = -0.01$, $P < 0.0001$, Fig. 14). The age of willow tits ($b = 0.60$, $P = 0.26$), sex ($b = -0.44$, $P = 0.40$), tarsus length ($b = 0.02$, $P = 0.59$), wing length ($b = -0.044$, $P = 0.74$) and body mass ($b = 0.10$, $P = 0.52$) did not contribute to *Plasmodium* infection (Nagelkerke's $R^2 = 0.589$, $P < 0.001$).

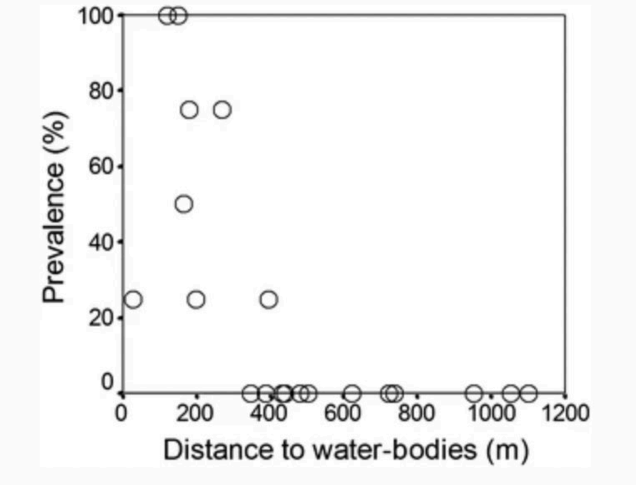

Figure 14. Relationship between distance to the nearest water bodies and prevalence of *Plasmodium* in willow tits.

3.7. Survival of wintering crested tits and willow tits in relation to distance to nearest water bodies (III)

A total of 69 out of 86 (80.23 %) crested tits and 61 out of 83 (73.49 %) willow tits survived, which did not reveal any significant differences in survival rates between willow (22 found dead or disappeared) and crested tits (17 found dead or disappeared; Fisher's exact test, $P = 0.37$).

The proportion of crested tits in flocks that survived until the next breeding season significantly correlated with the distance from the water bodies ($r = 0.74$, $n = 20$, $P < 0.0001$, Fig. 15). We found that survival of both adult crested tits ($r = 0.62$, $n = 20$, $P = 0.004$) and young individuals ($r = 0.75$, $n = 20$, $P < 0.0001$) increased away from water bodies.

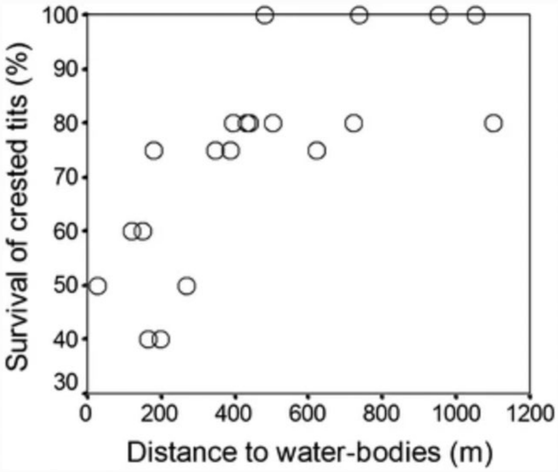

Figure 15. Correlation between distance to the nearest water bodies and overwinter survival of crested tits.

Willow tits also survived significantly better further from the lakes and bogs ($r = 0.79$, $n = 20$, $P < 0.0001$, Fig. 16). Both adult willow tits ($r = 0.58$, $n = 20$, $P = 0.008$) and young willow tits ($r = 0.83$, $n = 20$, $P < 0.0001$) survived significantly better away from the water bodies.

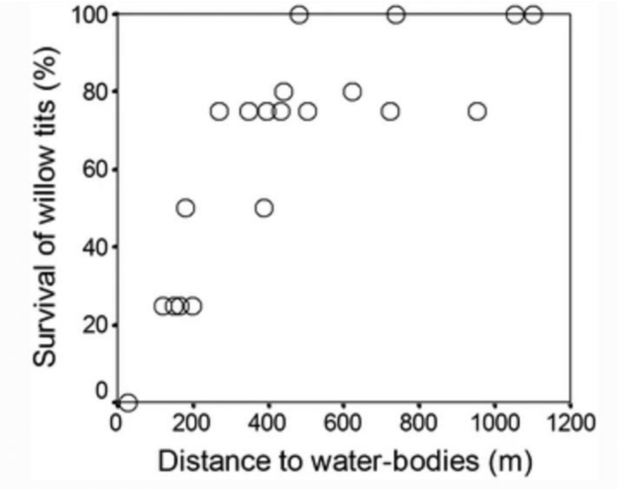

Figure 16. Correlation between distance to the nearest water bodies and overwinter survival of willow tits.

3.8. Survival association with infection status (III)

Un-infected crested tits survived (69 survived and 2 disappeared) significantly better than infected individuals (2 survived and 13 disappeared; Fisher's exact test, *P* = 0.0001). Non-infected willow tits also survived significantly better (54 survived and 2 disappeared) than willow tits infected (6 survived and 20 disappeared; Fisher's exact test, *P* = 0.0001).

3.9. Links between infection status and the predation by pygmy owls (III)

Thirty individual crested tits and willow tits were found in caches of pygmy owls. Thirteen crested tits were found cached by pygmy owls in nest boxes and all of them were infected individuals (Fisher's exact test, *P* = 0.044). Seventeen willow tits were found in caches of pygmy owls (16 infected vs. 1 un-infected; Fisher's exact test, *P* = 0.022), showing that pygmy owls mostly depredated infected willow and crested tits.

4. DISCUSSION

4.1. The synopsis of the results (I, II, III)

The results of this thesis show that ecological traps may occur not only in anthropogenically altered environments, but also in the areas affected by pest insects (**I**). The research done in this thesis also shows that habitats located near areas of high concentration of disease vectors can represent ecological traps, because breeding near water bodies may affect birds' condition (**II**), winter survival (**III**), predation pressure (**III**) and reproductive fitness (**II**).

4.2. Pest insect outbreaks and nest boxes as human-created ecological traps for cavity-nesting birds (I)

Study **I** shows that habitat quality of wild organisms can be impaired and habitats can be transformed in low-quality patches or even ecological traps caused not only by humans alone. It is shown that forests damaged by pest insects are transformed into ecological traps in such cases when artificial nest boxes are provided for the hole-nesting birds. While installing nest boxes is considered a simple and traditional way of attracting insectivorous birds to the areas of pest outbreaks (Jedlicka *et al.* 2011), leaf eating larvae of pest insects significantly reduce both, the total leaf area and even kill the trees. Since these activities reduce the total number of insects other than forest pests, this may significantly affect the total amount of food available for insectivorous birds and lower their reproductive fitness measured as fledgling numbers. Thus, the attraction of birds to forest patches occupied by outbreaking insects leads to maladaptive outcomes.

Notably, cavities are among the most important cues for habitat selection of cavity-nesting birds (Hildén 1965). Cavities and holes probably represent a super stimulus the birds cannot resist, making the impaired area attractive and raising the density of nesting birds well above the capacity the area can sustain. In this way, birds can be attracted independent of the actual number of resources available in the habitat (Mänd *et al.* 2005; Kilgas *et al.* 2007) causing malnutrition, starvation and even the death of nestlings of cavity-nesting birds. Therefore, providing surplus nest boxes to attract cavity-nesting birds to the areas of insect outbreaks can create ecological traps or sink habitats that are preferred habitats where individual fitness does not increase, or where mortality exceeds the birth rate (Kokko & Sutherland 2001; Hale *et al.* 2015).

The results of this study indicate that attracting cavity-nesting birds should be done with caution, because it may negatively impact birds' nutritional status and reproductive fitness.

These findings may have important conservation and management implications. First, although cavity-nesting birds are easy to attract to particular areas where they can be used as biological control agents to fight agricultural and forestry pests, it is important to discuss the extent to which it is ethical to lure birds to ecological traps. It is equally important to develop the theory of ecological traps, because of our limited ability to predict the formation of ecological traps, identify them when they do exist and to mitigate their impact (Robertson & Hutto 2006; Hale & Swearer 2016). However, we show that forest patches deteriorated by pest insects are easy to identify, which may help to prevent the attraction of insectivorous birds to the area of the ecological trap. Our results also raise the question of whether other human activities have the potential to turn large forest areas into ecological traps. For example, if modern forestry measures such as regular removal of understory trees and bushes from the plantations of coniferous forests reduces biomass of insects, and simultaneously erecting nest boxes for insectivorous birds increases the density of birds above naturally occurring levels, it might form ecological traps at the level of populations, environmental niches and ecosystems (Lindenmayer *et al.* 2008; Hale *et al*. 2015; Hale & Swearer 2016).

The results of this study also highlight the need to balance conservation efforts with research on habitat quality and the carrying capacity of ecosystems. For example, ecological traps may ruin an investment in the conservation of a species if the area contains too many competitors (*e.g.*, in high biodiversity spots) or its future quality is compromised. Ecological traps, such as low-quality forests may also decrease landscape connectivity even if these traps result in minor immediate fitness consequences (Sánchez-Mercado *et al.* 2014; Hale *et al.* 2015). Low genetic heterogeneity of organisms in these areas can further decrease their fitness and reduce the success of conservation measures (Prunier *et al.* 2017).

4.3. Forest water bodies as causes of ecological traps during the breeding season (II)

Overall, our results show that the forests near water bodies constitute an ecological trap for the birds that attempt to breed in the floristically diverse tree stands around lakes, streams and bogs. 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 (Jokimäki *et al.* 1998), while not being able to estimate the risks associated with blood parasite vectors that reproduce in the nearby water bodies. The higher numbers of parasite vectors and higher incidence of infections can lead to fledgling malnutrition, lower survival and low recruitment rate, suggesting the role of haemosporidian parasites and stress in determining the habitat quality of breeding birds (Illera *et al.* 2017; Muriel *et al.* 2021; Pigeault *et al.* 2023).

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 (Dale *et al.* 1996), the fitness of the birds 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 (Magrath 1991; Marzal *et al.* 2005). It has been known that *Haemoproteus* and *Plasmodium* parasites cause various adverse physiological and growth effects on their hosts (Marzal *et al.* 2005; Ishtiaq *et al.* 2008). Wild animals show sickness behaviours, which make them more exposed to predation risk, and they are less efficient in finding food during acute stages of haemosporidian infection (Krams *et al.* 2013; Gutiérrez-López *et al.* 2015). 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.

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 the 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 (Elbers *et al.* 2015), 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 (Carter *et al.* 2000; Thomas *et al.* 2013; Elbers *et al.* 2015; Kluiters *et al.* 2015; Brand *et al.* 2017), 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 (Wiersch *et al.* 2007; Dubiec *et al.* 2018; Jones *et al.* 2018), this study showed that *Haemoproteus* prevalence, *Haemoproteus* parasitemia, *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.

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 (Krams *et al.* 2001; Rytkönen & Krams 2003). 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 (Mänd *et al.* 2000; Dhondt *et al.* 2001). Thus, despite choosing the highest quality habitats possible, pied flycatchers had higher haemosporidian prevalence, the most intense parasitemia and 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, suggesting ecological traps around forest water bodies.

4.4. Haemosporidian parasite infections and survival of wintering territorial parids (III)

Some previous studies have already demonstrated a negative relationship between the distance from forest lakes and streams, and the prevalence of haemosporidian parasites during the reproductive season of passerine birds (Wood *et al.* 2007; Krams *et al.* 2010, 2012b). This study on crested tits and willow tits, wintering in territorial winter groups with the closed social system, represents the first evidence showing a similar relationship outside the reproductive season of birds. Importantly, the results suggest an overlooked issue affecting winter mortality in temperate passerines. In brief, this study links the infection status of individual birds and their overwinter survival by showing that overwinter survival of members of mixed-species tit groups is significantly lower in vicinities close to forest water bodies such as lakes and bogs.

The results of this study show that wintering territories located far from the water bodies may represent a safer environment in terms of pathogen risk, especially in willow tits. The probability of acquiring of a haemosporidian infection in both parid species in late summer and early autumn was much lower in areas distant from the forest lakes and bogs than in territories close to the water bodies. Noteworthy, the intensity of *Plasmodium* infection decreased further from water bodies in willow tits. Although we did not find any direct cost linked with disease incidence *per se*, the results of this study show that infected hosts incur severe mortality costs via predation. We demonstrate a positive association between infection and mortality by showing that infected willow and crested tits constitute a substantial part of the diet of wintering pygmy owls. Some studies have shown that diseased prey is easier to catch than healthy individuals and that predators will often consume infected prey (Packer *et al.* 2003; Johnson *et al.* 2006; Duffy & Sivars-Becker 2007). This is probably, because the infected individuals are less vigilant due to their seemingly elevated energy requirements under low ambient temperature.

Overwinter survival did not differ between adults and young individuals, and between sexes of crested and willow tits. However, we found a significantly lower prevalence of *Haemoproteus* infection in crested tits than in willow tits. Moreover, we did not find any *Plasmodium* infection in crested tits. A possible explanation would be a better immune response of crested tits against *Plasmodium* parasites, as many bird species may have efficient immune responses against blood parasites (*e.g.,* Krams *et al.* 2013).

Another explanation for the low prevalence of *Haemoproteus* and the lack of *Plasmodium* might be a dominance rank-related distribution of members of tit groups within the tree canopy. Within mixed-species flocks of forest parids, a linear dominance hierarchy exists in which crested tits dominate willow tits, while males, with a few exceptions, dominate females and adults dominate juveniles (Ekman 1979; Hogstad 1987). Thus, age is a rough equivalent of social rank in wintering parids (Ekman 1989). It is noteworthy that the presence of dominant crested tits in wintering flocks is important in determining the fattening strategies of willow tits (Krams 1998), a crucial factor not only for wintering birds, but also migrating birds. In the tree canopy, dominant crested tits prefer the upper parts, while subordinate willow tits are forced to forage in the lower canopy, a part of the tree that may be more exposed to attacks of parasite vectors. Although the abundance/presence of insect vectors was not quantified in this study, it was shown that numerous species of mosquitoes are recognized to preferentially inhabit lower parts of tree canopies (*e.g.*, Anderson *et al.* 2004; Savage *et al.* 2008). Vertical stratification is also influenced by humidity, temperature and light (Clements 1992), which may make crested tits foraging in the upper canopy less vulnerable to mosquito attacks than willow tits in the middle or lower canopy (Černý *et al.* 2011). Moreover, it has been shown that midges prefer to bite near the ground and are uncommon at heights more than about 3 m from the ground (Mitchell 1982), making these parasite vectors less important to dominant individuals high in the canopy.

To sum up, the results of this field study show that overwinter survival of members of mixed-species flocks of parids depend not only on the availability of food, the presence of predators and dominance rank (Krams 1998; Krams *et al.* 2001), but also on parasite infections and proximity to areas where parasite vectors reproduce. We show a lower prevalence of blood parasites in dominant members of mixed-species tit flocks foraging in the upper parts of the canopy (Krams 2001). It indicates that some forest and canopy parts may be less accessible to parasite vectors and more preferable to birds (Ekman 1987; Krama *et al.* 2008), while areas close to the forest lakes and other water bodies might become ecological traps for breeding and wintering birds. We suggest that foraging and perhaps nesting, and singing in higher parts of the canopy might be beneficial in terms of lower parasitism and higher survival, because of supposedly lower densities of blood parasite vectors there. Overall, our study shows the importance of linking the research on spatial distribution and life history of hosts, and the distribution of vectors of their haemosporidian parasites (Valkiūnas 2011; Oakgrove *et al.* 2014). Finally, the effect of predation on the distribution of parasites and virulence evolution is addressed in a few studies. Choo *et al.* (2003) and Morozov and Adamson (2011) suggested that adding predators into host–parasite systems can result in evolutionary suicide in the parasite. The results of this study support this theoretical idea. As an explanation for the rarity of relapses in chronically infected individuals during the next breeding season, we suggest that most infected hosts are depredated during the wintering season. Future correlational and experimental studies are required to reveal the impact of predation on the resulting outcome of virulence evolution and its epidemiological consequences in detail.

SUMMARY AND CONCLUSIONS

The use of nest boxes to attract cavity-nesting birds to areas of insect outbreaks is a traditional measure to protect forest ecosystems. However, these forests can become deteriorated by pest insects so that the attracted birds lack sufficient resources to feed their offspring. In the first study (**I**), we conclude that (1) ecological traps can arise in forest areas where humans attract insectivorous cavity-nesting birds to fight outbreaking insects. By installing nest boxes, the density of birds can be easily raised above naturally occurring densities, thus exceeding the carrying capacity of bird habitats. Our results (**I**) suggest that the use of cavity-nesting birds in the biological control of insect pests should be done with caution, because it may negatively impact birds' reproductive fitness in areas of unintended ecological traps.

The second study (**II**) 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. (2) 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.

The results of the third study (**III**) show that members of mixed species winter groups of parids staying further from the forest water bodies and spending more time foraging in the upper parts of the canopy have higher chances of survival into the next breeding season. (3) This suggests that different forest and canopy areas may differ in terms of parasite risk and associated mortality. Finally, we found that the infection status of parids increases the probability of predation by the pygmy owl. (4) We conclude that distance from water bodies and foraging location in the forest canopy may affect the intensity of parasite infection with fitness consequences in wintering parids.

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POPULATION ECOLOGY – ORIGINAL RESEARCH

Ecological traps: evidence of a fitness cost in a cavity-nesting bird

Ronalds Krams[1,2] · Tatjana Krama[1,2] · Guntis Brūmelis[3] · Didzis Elferts[3] · Linda Strode[3] · Iluta Dauškane[3] ·
Severi Luoto[4,5] · Agnis Šmits[6] · Indrikis A. Krams[1,7,8]

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Abstract

Habitat quality has direct effects on the evolutionary fitness of breeding organisms, which is why it is believed that animals tend to have an evolved preference for the best possible habitats. However, some animals may mistakenly choose to reproduce in habitats that decrease their fitness, resulting in 'ecological traps'. In this study, we tested whether great tits (*Parus major*) attracted to areas affected by outbreaks of the great web-spinning sawfly (*Acantholyda posticalis*) had fitness detriments characteristic of ecological traps. Sawfly larvae consume pine needles, which decreases resource availability for birds co-habiting the forest. Using artificial nesting sites, we found that great tits inhabiting areas of sawfly outbreaks had similar clutch sizes as tits breeding in healthy forest patches; however, the fledgling number was significantly lower, and fledgling condition was worse in the damaged forests. While moth larvae are the most important food for bird nestlings, the forest patches damaged by sawflies had lower larval biomass. Although most ecological traps occur in environments altered by humans, this study shows that pest insects can lower habitat quality, forming ecological traps. Our results indicate that attracting cavity-nesting birds should be done with caution because it may negatively impact birds' nutritional status and reproductive fitness.

Keywords Ecological traps · Cavity-nesting birds · Great tits · Fitness cost · Resources · Behavioral ecology

Introduction

Evolution creates variation in the genetic tapestry of life via natural selection. One of the principal drivers of natural selection is adaptation to different environments or ecological niches: some genetic variants become favored over others in certain environments (Schluter 2009; Luoto 2019a, b; Rees et al. 2020), resulting in variation in the diverse forms that life takes (Darwin 1859). Yet when environments change rapidly, and when organisms lack adequate genetic, behavioral, and/or phenotypic plasticity, organisms may end up choosing habitats that are detrimental to their fitness. Such outcomes are termed 'ecological traps' (Sherley et al. 2017; Sun et al. 2020). Ecological traps are becoming increasingly salient features in behavioral ecology because of human-induced environmental modifications (Hale and Swearer 2016). Ecological traps have three general criteria: (i) individuals prefer one habitat over another (a 'severe' trap) or equally prefer multiple habitats (an 'equal preference' trap); (ii) fitness (or a reasonable surrogate measure) differs between habitats; and (iii) fitness is lower when animals exploit the (equally) preferred habitat (Robertson and Hutto 2006; Hale and Swearer 2016). There are various ways

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✉ Indrikis A. Krams
indrikis.krams@ut.ee

[1] Department of Biotechnology, Daugavpils University, Daugavpils 5401, Latvia

[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, Riga 1004, Latvia

[4] English, Drama and Writing Studies, University of Auckland, Auckland 1010, New Zealand

[5] School of Psychology, University of Auckland, Auckland 1010, New Zealand

[6] Latvian State Forest Research Institute "Silava", Salaspils 2169, Latvia

[7] Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia, Riga 1004, Latvia

[8] Institute of Ecology and Earth Science, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

by which ecological traps arise. Animals may mistakenly prefer habitats where their fitness is reduced because they have not experienced such conditions during their individual and evolutionary history (Hale and Swearer 2017). Animal survival and reproduction can also be impaired in habitats restored by humans if management activities result in an ecological trap (Hale and Swearer 2017).

Insects are crucial parts of forest ecosystems worldwide where they serve as food sources to other forest dwellers and perform the role of pollinators, omnivores, herbivores, carnivores, and decomposers. Insects often attack forest crops by decreasing timber resources. Several forest pest species experience population cycles in which populations remain low for several years and are followed by outbreaks (population explosions). Outbreaks of insects are considered to be major sources of habitat disturbance in forest ecosystems (Barbosa et al. 2012; Moulinier et al. 2013), altering vegetation characteristics (Dennison et al. 2010; Man and Rice 2010; Yang 2012; Karlsen et al. 2013), organismal interactions, and structure and density of consumer populations (Vindstad et al. 2015).

Pest insects and their outbreaks can be traditionally controlled by insecticides. However, agrochemicals often harm biological diversity, including all other beneficial arthropods, which substantially impairs ecosystem services provided by biodiversity (Daily and Matson 2008). Regulation of pests by attracting and enhancing natural enemies of insects is an alternative approach used in agriculture and forestry practice (Swinton et al. 2007; Tscharntke et al. 2012). Bird predation has an important role in biological control (Holmes et al. 1979; Langelier and Garton 1986; Duan et al. 2015) by reducing numbers of pest insects and significantly decreasing the frequency of outbreaks (Solomon et al. 1976; Torgersen et al. 1984). Birds have also been shown to reduce pest damage and substantially increase commercial fruit and coffee production (Mols and Visser 2002, 2007; Mols et al. 2005; Kellermann et al. 2008; Johnson et al. 2010; Jedlicka et al. 2011).

Biological control by provisioning nest boxes for insectivorous birds is a commonly used approach to attract hole-nesting birds, especially in Europe (Fischer and McClelland 1983; Gosler 1993; Kirk et al. 1996; Tilgar et al. 1999; Mols and Visser 2002, 2007; Mols et al. 2005; Mänd et al. 2005). The use of nest boxes has promoted biological research and led to significant progress in our understanding of ecological, physiological, and behavioral processes in birds including the impact of climate change on biodiversity (Lambrechts et al. 2010; Møller et al. 2014; Vaugoyeau et al. 2016; Samplonius et al. 2018). Putting up nest boxes is a simple method to encourage avian populations at the sites of insect outbreaks (Mols and Visser 2002; Jedlicka et al. 2011). Some birds, such as great tits (*Parus major*), show a striking preference for artificially made nest boxes over natural tree cavities (Drent 1984) because artificial nest boxes are constructed to minimize nest predation, humid microclimate, nest soaking, and improve nest illumination (Wesołowski 2011; Maziarz et al. 2016). Provisioning of nest boxes makes it easy to compensate for naturally low availability of cavities, which is a limiting factor especially in forest plantations. As cavities are among the most important cues for habitat selection of cavity-nesting birds (Hildén 1965), abundant nest boxes make an area attractive and thus the density of nesting bird can be raised well above naturally occurring densities. Birds can be attracted independent of the actual amount of resources available in the habitat (Mänd et al. 2005; Kilgas et al. 2007). This makes it possible to attract cavity-nesting birds to ecological traps or sink habitats that are preferred habitats where individual fitness does not increase or where mortality exceeds the birth rate (Gates and Gysel 1978; Delibes et al. 2001; Donovan and Lamberson 2001; Kokko and Sutherland 2001; Schlaepfer et al. 2002; Kristan 2003).

Interestingly, some bird species positively respond to the increased density of leaf-eating autumnal moth (*Epirrita autumnata*) larvae because they provide an unlimited food source for adult individuals and their offspring during outbreaks. This causes breeding nomadism in the brambling (*Fringilla montifringilla*) by attracting this passerine bird to birch forests affected by outbreaking *E. autumnata* (Mikkonen 1983; Hogstad 1985; Lindström 1987). However, some other birds do not react at all or respond negatively to outbreaks by *E. autumnata* (Enemar et al. 2004). For example, the redpoll (*Carduelis flammea*) is to some extent dependent on birch seeds, a food supply that is not available in subalpine birch forest affected by *E. autumnata* (Enemar and Nyström 1981). This suggests that outbreaking insects deteriorate the environment even though their larvae constitute a considerable part of the food of local birds (Hogstad 1988). The grazing larvae, for instance, affect the vegetation in the form of defoliation, reduced flowering, and seed production which may have a negative effect on other arthropods, lowering the overall quality of the environment. Finally, this reduces the number of outbreaking insects themselves and forces most of the birds to leave the area (Selås et al. 2001; Enemar et al. 2004).

Putting up nest boxes in the forest patches affected by insect outbreaks may attract cavity-nesting birds to ecological traps. In this study, we tested whether great tits breeding in pine forests heavily damaged by outbreaking of the great web-spinning sawfly (*Acantholyda posticalis*) suffer fitness costs. The great tit is a common bird species in Latvia and readily accepts nest boxes to breed in any kind of forest and parkland. Within the breeding season, great tits mainly forage for insect larvae, which is the preferred food for their nestlings and fledglings (Rytkönen and Krams 2003). We provided nest boxes in mature Scots pine (*Pinus sylvestris*) forest stands both affected (loss of foliage) and non-affected by sawflies. Natural cavities were hardly available in either environment. Hole-nesting birds have been traditionally considered as predators that can affect defoliator pest outbreaks, which is why foresters traditionally put up nest boxes in forest stands affected by the sawfly and moth pest species (Bičevskis 2005; Jankevica 2008; Šmits 2005).

Great web-spinning sawfly adults emerge from the soil and females lay eggs on needles of Scots pine in June (Voolma et al. 2016). Sawfly larvae consume the needles of pines and feed on the needle substrate until the beginning of August. At the fourth larval instar stage the larvae move to the soil where they stay for two to five years before they emerge after a short pupation (Ghimire et al. 2013). The highly variable larval stage makes outbreaks of great web-spinning sawflies unpredictable (Ghimire et al. 2013). Importantly, patches damaged by a web-spinning sawfly outbreak are easy to distinguish from healthy patches because in the damaged areas pines are strikingly defoliated.

While we predicted similar clutch sizes between the patches damaged by web-spinning sawflies and healthy patches, we expected smaller fledgling numbers, lower fledgling body mass, and shorter tarsus lengths due to malnutrition in the nest boxes located in the patches damaged by sawflies. We also studied larval biomass in patches occupied by great tits to estimate food resources available to their nestlings. As larval biomass can be expected to be related to the amount of available foliage, we used estimates of live tree crown volume and canopy cover as indirect measures of larval biomass (Brūmelis et al. 2020).

Materials and methods

Study area, nest boxes, and birds

The breeding ecology of great tits was monitored near Daugavpils, southeastern Latvia (55.55° N, 26.34° E). The study area covers Scots pine stands affected by an on-going mass outbreak of the great web-spinning sawfly. The outbreak was first observed in summer 2013. This is a second observed outbreak of this pest in Latvia. The previous outbreak was observed some 40 km eastwards during 1966–1982. Prolonged outbreaks are typical for great web-spinning sawflies. Years of intensive flight are followed by years when the majority of larvae fall in diapause. Consequently, years with heavy tree defoliation are followed by years when trees are able to partly recover their foliage. This study was conducted in 2019 when flight activity was low and the larvae of great web-spinning sawflies were hardly available as a food resource for birds in the spring–summer period.

Nest boxes were mounted on pine trunks at a height of about 3.0 m. The internal size of the nest boxes was 0.13 × 0.13 × 0.25 m, and the diameter of the entrance was 0.036 m. Breeding success, fledgling number, their body mass, and tarsus length were recorded in two contrasting types of forest patches—the pine forest damaged by web-spinning sawflies and a nearby healthy pine forest. We chose six areas in the affected pine forest and five areas in the nearby healthy forest (Fig. 1). We put up 12 nest boxes in each of these patches (72 nest boxes in the affected forest and 60 nest boxes in the healthy forest). Out of 132 nest boxes, great tits occupied 34 nest boxes in the damaged forest and 31 nest boxes in the healthy forest (65 nest boxes in total). Great tit offspring successfully fledged in 59 nest boxes (30 nest boxes in the damaged areas and 29 nest boxes in the healthy areas). The total area of the damaged forest was c. 120 ha. The total size of studied patches with nest boxes was c. 3.8 ha. The distance between study patches (each containing 12 nest boxes) was at least 480 m. To avoid competition (Dhondt 2011), the distance between neighboring boxes was c. 50 m in each of the 11 study patches.

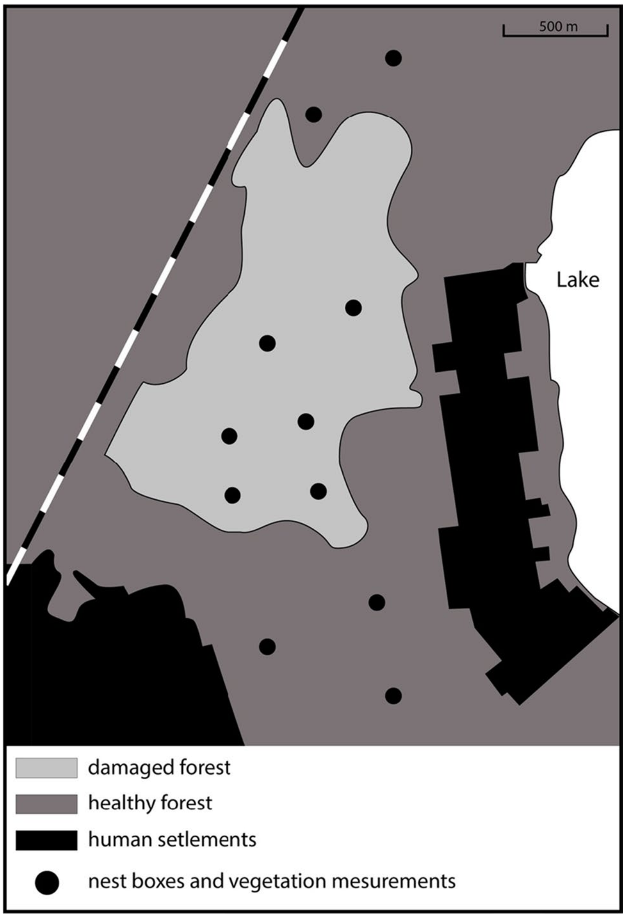

Fig. 1 The study sites in a pine forest in the surroundings of Daugavpils. Filled circles denote the sites where pine condition was studied and where the nest boxes were located

The nest boxes were checked regularly to record basic breeding parameters, such as the number of eggs and the number of fledglings, which is an indication of breeding success. To assess offspring quality, all nestlings were weighed with a Pesola spring balance to a precision of 0.1 g, and their tarsi were measured with sliding calipers to the nearest 0.1 mm on day 15 posthatch (Kilgas et al. 2006).

Food resources

We estimated the amount of food resources available in each forest patch by using the frassfall method (Rytkönen and Krams 2003). In brief, frass production by larvae was measured using plastic funnels (diameter 35 cm) with a paper coffee filter (size 1 × 4) attached to each funnel. The filter lets rainwater go through but frass produced by herbivory larvae is retained inside the filter. We used three funnels in each study patch ($n = 33$). The funnels were attached to trunks of randomly chosen pines, and the distance between the funnels was c. 60 m. As soon as the first nestlings in the patch reached the age of 7 days, the funnels were placed for a period of 4 days. The filters with the frass were preserved in a freezer. The frass production was determined by counting the frass items in each filter, and the average diameter of the frass items was determined by measuring randomly sampled frass items in each filter with an ocular micrometer. We estimated larval biomass from frass dry mass by using an allometric relationship between frass diameter and frass dry mass (Rytkönen and Orell 2001) and the equation by Tinbergen and Dietz (1994). As we could not discriminate between frass produced by larvae of moths and sawflies (Zandt 1994), this part of the research provided an estimation of the total food resources available in each forest patch.

Tree canopy in the patches of sawfly outbreak and in the unaffected patches

We studied how the condition of forest patches affects breeding parameters of great tits. We distinguished between healthy (< 25% foliage loss), damaged (25–75% foliage loss), and dead trees (< 25% foliage remaining) (Brūmelis et al. 2020). We measured the following three condition parameters: (1) total canopy cover of pines (%), (2) the relative number of dead and dying trees with 75–100% loss of needles due to web-spinning sawfly damage (%), and (3) the total tree crown volume ($m^3\ ha^{-1}$). In a recent study on allometric relationships between tree crown parameters, we proposed that, while tree crown parameters are usually ignored in studies on food resources due to difficulty of measurement, there are simple-to-measure parameters that could be used in studies to estimate food resources of animals (Brūmelis et al. 2020). The canopy cover is the layer formed by the branches and leaves of trees. The cover has higher values when it is continuous and much smaller when it is discontinuous. The relative number (%) of dead trees reflects the rate of damage done by a pest. High amounts of leaf (needle) damage eventually leads to the death of a tree. The total volume of tree crowns in the patch is important because it reflects the total amount of substrate that insectivorous birds can use to collect their food.

Four circular plots sized 10 m^2 were set up in azimuth directions at a 50-meter distance from a central location in each patch. Canopy cover was estimated with a gridded concave mirror (Forest densitometer) in each plot in four azimuth directions at a central point offset at least by a 2-meter distance from the nearest tree. Briefly, the grid on the mirror is used to count points at crossing lines that coincide with the tree canopy on the mirror, calculated as percent canopy cover (Brūmelis et al. 2020).

In each plot, diameter (DBH) of all trees at a height of 1.3 m was measured. In addition, measurement of tree crown parameters (height to top and base of the live tree crown, and width of the tree crown in two perpendicular directions) were made in each plot for 2–4 trees with different size and extent of damage. A Haglof VL5 vertex was used to measure height to top and base (lowest living branch) of the live tree crown. A GRS densitometer was used to precisely locate edge of the crown for width measurements. Tree crown measurements were made for 76 healthy and 16 damaged (more than 25% of needles lost) pine trees. Tree crown volume was estimated as an ellipsoid, as suggested for practical purposes for Scots pine (Rautiainen et al. 2008). The allometric relationship between stem diameter and crown volume for sampled trees for crown parameters was used to estimate volume for all trees in plots using an exponential regression model, separately for healthy [volume = 10.529588*EXP(0.068715*DBH)] and damaged [volume = 3.85498*EXP(0.09189*DBH)] trees. The exponential model was found to best explain the relationship between DBH and crown volume ($R^2 = 0.525$ and $R^2 = 0.605$ for healthy and damaged trees, respectively), and was superior or similar to a linear and power relationship, respectively. For the calculations, we also included data from 82 pine trees measured in this study area (Brūmelis et al. 2020). The total tree crown volume per hectare in the stands was then estimated.

Data analyses

We used a Bayesian linear mixed-effects models (LMER) and generalized linear mixed-effects models (GLMM) as implemented in the R 4.0.2. (R Core Team 2020) library brms (Bürkner 2017) to analyze the effects of stand parameters (independent variable) on the bird parameters (dependent variable). Separate models with one fixed factor and one dependent variable were implemented for each combination of stand parameters: total canopy cover, rate of dead trees, total canopy volume; and bird parameters: clutch size (Poisson GLMM), proportion of fledglings (binary logistic GLMM), body mass (LMER), tarsus length (LMER). In all models plot ID was set as a random factor to account for pseudoreplication. For models with body mass and tarsus length, nest ID was added as a nested random factor within plot ID. The number of iterations was set to 2500 for each of four chains. Rhat values (all close to ~ 1.00) were used to assess the convergence of the models. *P* values for the models were calculated with R library bayestestR (Makowski et al. 2019) function p_map. Spearman correlation analysis was used to assess relationships between stand parameters (canopy volume, total pine canopy cover, the proportion of dead trees) and larval biomass.

Results

Larval biomass in damaged and healthy forest patches

The overall biomass of canopy-dwelling insect larvae during the nestling period of great tits was significantly associated with sawfly damage. Larval biomass in the canopy increased in patches with greater canopy volume ($r_s = 0.882$, $P = 0.001$; Fig. 2A), increased in patches with greater total pine canopy cover ($r_s = 0.945$, $P < 0.001$; Fig. 2B), and decreased in patches with a high number of dead trees ($r_s = -0.934$, $P < 0.001$; Fig. 2C).

Clutch size

Sawfly damage was not significantly associated with clutch size in great tits. Clutch size did not depend on the total pine canopy cover [Slope estimate: – 0.000, Credibility interval (CI): (– 0.007, 0.007), $P = 1.00$, Fig. 3A], the proportion of dead trees [Estimate – 0.000, CI (– 0.002, 0.002), $P = 0.984$, Fig. 3B], nor on total canopy volume [Estimate – 0.004, CI (– 0.087, 0.078), $P = 0.992$, Fig. 3C]. We did not observe second clutches of great tits in the forest damaged by the outbreak of great web-spinning sawflies, while 58.6% ($n = 17$) of the great tits had second clutches in the forest unaffected by the pest.

Number of fledglings

The rate of sawfly damage reduced the proportion of the young fledged per clutch. The proportion of fledglings per clutch increased with the total pine canopy cover [Estimate 0.099, CI (0.062, 0.135), $P < 0.001$, Fig. 4A], decreased with the number of dead trees [Estimate – 0.033, CI (– 0.040, – 0.027), $P < 0.001$, Fig. 4B], and increased with total canopy volume [Estimate 0.973, CI (0.371, 1.565), $P = 0.016$, Fig. 4C].

Fledgling body mass

The extent of damage caused by the sawfly outbreak was significantly associated with fledgling body mass in great tits. We found that body mass of fledglings increased with the total pine canopy cover [Estimate 0.033, CI (0.017, 0.048), $P < 0.001$, Fig. 5A], declined with increasing number of dead trees [Estimate – 0.012, CI (– 0.014, – 0.010), $P < 0.001$, Fig. 5B], and increased with the total canopy volume [Estimate 0.289, CI (0.006, 0.567), $P = 0.084$, Fig. 5C].

Fledgling tarsus length

Great web-spinning sawfly outbreak was significantly associated with fledgling tarsus length. We found that tarsus length of fledglings increased with the total pine canopy cover [Estimate 0.011, CI (0.001, 0.020), $P = 0.071$, Fig. 6A], declined with increased number of dead trees [Estimate

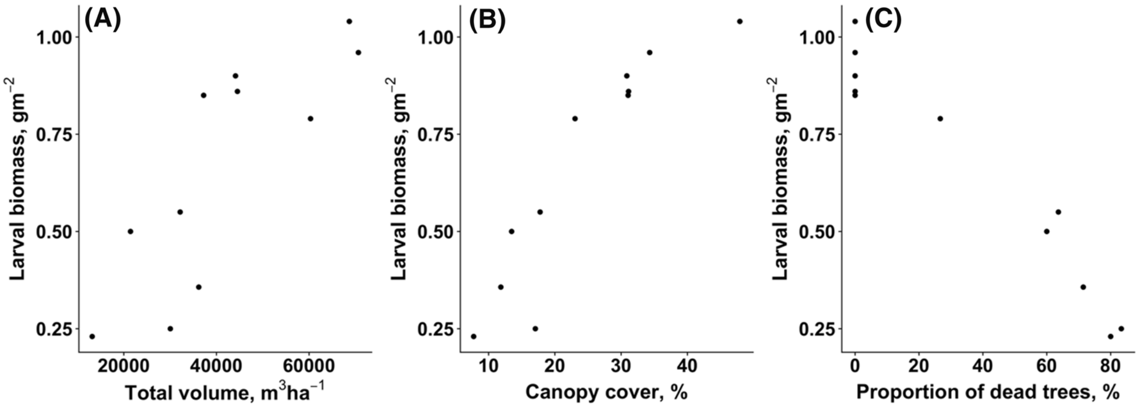

Fig. 2 Correlations between larval biomass and total canopy volume (**A**), total pine canopy cover (**B**), and rate of dead trees (**C**)

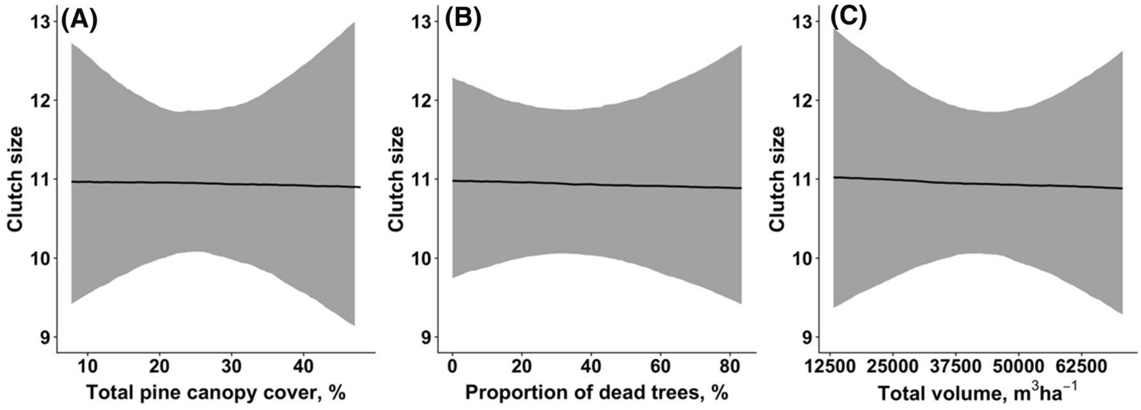

Fig. 3 Associations between the clutch size of great tits and total pine canopy cover (**A**), rate of dead trees (**B**), total canopy volume (**C**). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals

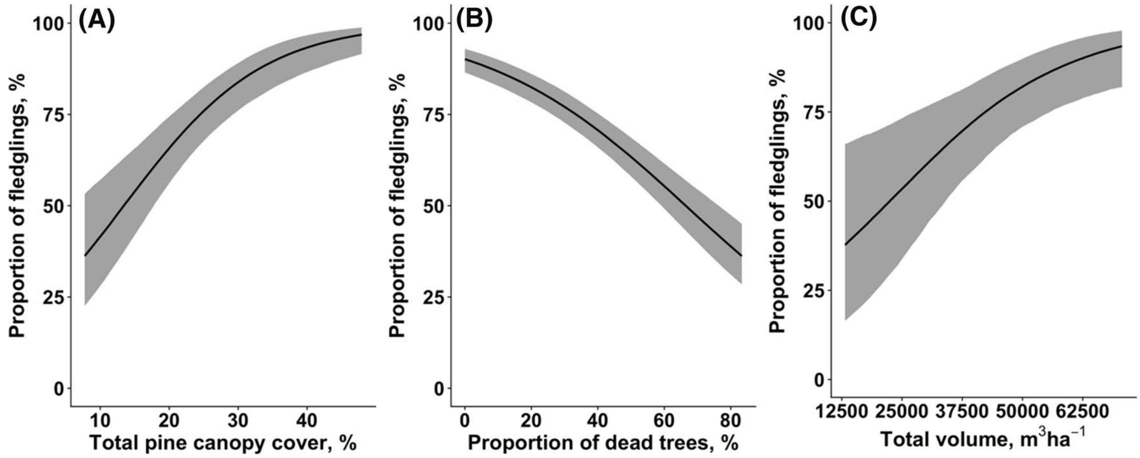

Fig. 4 Associations between the proportion of fledglings per clutch and total pine canopy cover (**A**), rate of dead trees (**B**), and total canopy volume (**C**). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals

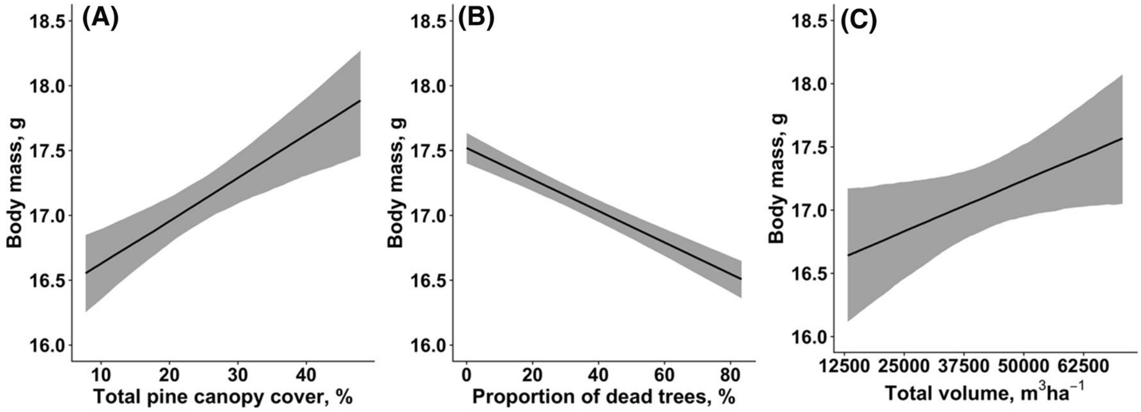

Fig. 5 Associations between fledgling body mass and total pine canopy cover (**A**), rate of dead trees (**B**), and total canopy volume (**C**). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals

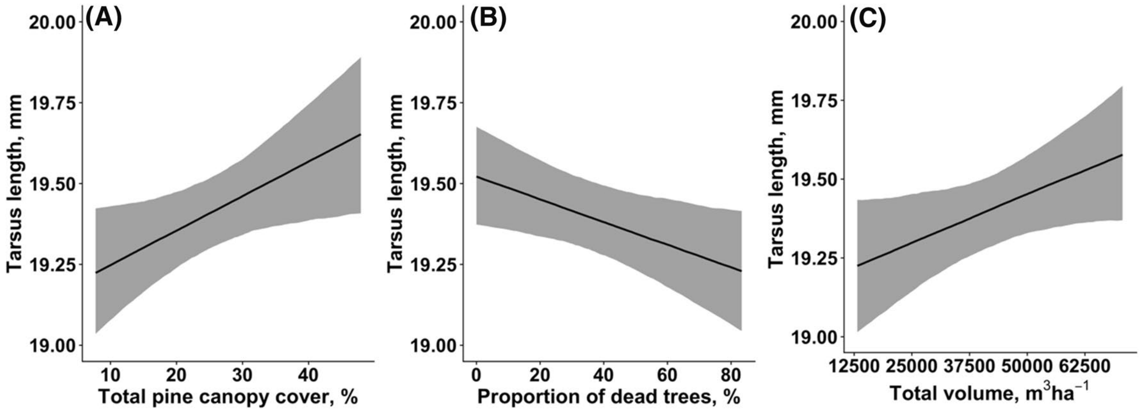

Fig. 6 Associations between fledgling tarsus length and total pine canopy cover (**A**), rate of dead trees (**B**), and total canopy volume (**C**). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent 95% credibility intervals

− 0.004, CI (− 0.007, − 0.001), $P = 0.061$, Fig. 6B], and increased with total canopy volume [Estimate 0.110, CI (0.000, 0.222), $P = 0.128$, Fig. 6C].

Discussion

Based on the canopy indices like tree crown volume and proportion of dead trees, the patches represented a gradient from severely damaged to healthy stands. Further, the strong correlations of larval biomass with tree canopy volume and canopy cover suggest that in similar studies, the easy-to-measure canopy parameters might be used a proxy for the amount of food resources. We found that clutch size of great tits did not statistically correlate with any of the canopy indices (used as an indirect representative of the outbreak of great web-spinning sawflies). This suggests that birds chose their breeding habitats based on the availability of cavities suitable for breeding. However, the number of fledglings was lower, and their condition was substantially poorer in the forest damaged by the sawfly outbreak. Larval biomass was significantly greater in the healthy forest area characterized by greater total canopy cover and total canopy volume and lower rate of dead trees than in the damaged forest. *A. posticalis* larvae develop later in the season when young birds have already fledged their nests and did not serve as a food source. Overall, our results indicate that the damaged forest area constitutes an ecological trap for the birds that attempted to breed in this type of forest.

'Severe ecological traps' occur when animals prefer to occupy poor-quality habitats over habitats of good quality. Ecological traps can generally arise when the behavior and preferences of the organism do not match its environment—a mismatch caused by serious changes in the environment of the organism while its behavior remains the same as before the environmental changes (Kokko and Sutherland 2001; Schlaepfer et al. 2002; Mänd et al. 2005; Hale and Swearer 2016). In this study, we deal with an ecological trap that meets all three criteria suggested by Robertson and Hutto (2006) and Hale and Swearer (2016). Cavities as the main limiting resource for hole-nesting birds can be completely absent in managed pine plantations where nest boxes are put up to compensate for the lack of natural cavities. It is important to note that habitat quality of wild organisms can be impaired, and habitats can be transformed in low-quality patches or even ecological traps caused not only by humans (Demeyrier et al. 2016). We show that forests damaged by pest insects are transformed into ecological traps in such cases when artificial nest boxes are provided for hole-nesting birds. While great tits are instrumental in fighting sawflies in the areas of their outbreaks, the attraction of birds to these forest patches leads to maladaptive outcomes and significantly decreases fitness parameters of the birds.

The results of this study suggest that the poor availability of insect larvae in the outbreak area makes food abundance a crucial factor in decreasing fitness parameters in breeding great tits. Great web-spinning sawfly causes substantial damage to pine canopies by eating their needles. In the great tit, insect larvae form up to 73% of the nestling diet (Rytkönen and Orell 2001) and this species is highly dependent on herbivorous insects and their larvae during the nestling period. However, outbreaking sawflies destroy most of the branches, weaken pines, and even kill individual trees, thereby making foraging substrate less available for next generations of sawflies and other herbivorous insects. The ability of adult great tits to compensate for low habitat quality is limited. This is because great tits primarily search for larvae and do not totally switch to some other, more abundant food during the nestling period (Robinson and Holmes 1982; Holmes and Schultz 1988). Another reason for the inability to compensate for low habitat quality is that the birds typically collect food for their nestlings within 50–70 m from the nest (Rytkönen and Orell 2001; Rytkönen and Krams 2003). The inability of parents to bring enough food, together with the low leaf eating larvae biomass in the patches affected by web-spinning sawflies, causes malnutrition of nestlings. They grow more slowly and are smaller at the time of fledging in the outbreak areas. Malnutrition and probably also competition between nestlings cause higher nestling mortality which results in a significantly lower number of fledglings in the outbreak area compared to the healthy forest.

One of the shortcomings of this study was that we could not estimate the fledgling survival and recruitment rate of great tits breeding in the damaged and healthy forest patches. Our results show that adult great tits have never attempted to have second clutches in the damaged forest. They left this area together with their fledglings as soon as their offspring fledged (*pers. obs.*). We did not continue this experimental study for one more year, which precluded us from estimating the recruitment rate in the outbreak area to compare this with recruitment rates in the healthy forest. We highly recommend that other researchers continue their studies for at least two breeding seasons of their study subjects to better understand the effects of ecological traps.

The results of this study may have important conservation and management implications. First, although hole-nesting birds are easy to attract to particular areas where they can be used as biological control agents to fight agricultural and forestry pests, it is important to discuss the extent to which it is ethical to lure birds to ecological traps. It is equally important to develop the theory of ecological traps because of our limited ability to predict the formation of ecological traps, identify them when they do exist, and to mitigate their impact (Hale and Swearer 2016; Robertson and Hutto 2006). However, we show that forest patches deteriorated by pest insects are easy to identify, which may help to prevent the attraction of insectivorous birds to the area of the ecological trap. Our results also raise the question of whether other human activities have the potential to turn large forest areas into ecological traps. For example, if modern forestry measures such as regular removal of understory trees and bushes from the plantations of coniferous forests reduces biomass of insects and simultaneously erecting nest boxes for insectivorous birds increases the density of birds above naturally occurring levels, it might form ecological traps at the level of populations, environmental niches, and ecosystems (Lindenmayer et al. 2008; Hale et al. 2015; Krama et al. 2015; Hale and Swearer 2016).

Finally, our results highlight the need to balance conservation efforts with research on habitat quality and the carrying capacity of ecosystems. For example, ecological traps may ruin an investment in the conservation of a species if the area contains too many competitors or its future quality is compromised. Ecological traps such as low-quality forests may also decrease landscape connectivity even if these traps result in minor immediate fitness consequences (Sánchez-Mercado et al. 2014; Hale et al. 2015). Low genetic heterogeneity of organisms in these areas can further decrease their fitness and reduce the success of conservation measures (Prunier et al. 2017).

Conclusions

The use of nest boxes to attract cavity-nesting birds to areas of insect outbreaks is a traditional measure to protect forest ecosystems. However, these forests can become deteriorated by pest insects so that the attracted birds lack sufficient resources to feed their offspring. The results of this study show that ecological traps can arise in forest areas where humans attract insectivorous cavity-nesting birds to fight outbreaking insects. Cavities are the main limiting resource for birds nesting in nest boxes. By installing nest boxes, the density of birds can be easily raised above naturally occurring densities, thus exceeding the carrying capacity of bird habitats. We found malnutrition and higher mortality of offspring in the forest area affected by insect outbreaks. Our results suggest that the use of cavity-nesting birds in the biological control of insect pests should be done with caution because it may negatively impact birds' reproductive fitness in areas of unintended ecological traps.

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Author contribution statement RK, TK, IAK and GB conceived and designed the study and participated in the drafting of the manuscript. TK, RK, GB, LS, ID, AŠ and IAK performed the study, collected and extracted data. TK, RK, GB, DE and IAK analysed data. LS, ID and SL participated in data analyses, results interpretation and drafting the manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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II PUBLICATION

II PUBLIKĀCIJA

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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 Elferts [3], Janīna Daukšte [4], Patrīcija Raibarte [4], Guntis Brūmelis [3], Iluta Dauškane [3], Linda Strode [3] 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

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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 nests 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 μL) 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× magnification for *Haemoproteus* and *Plasmodium* and at 500× 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 × 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 × 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 ~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)).

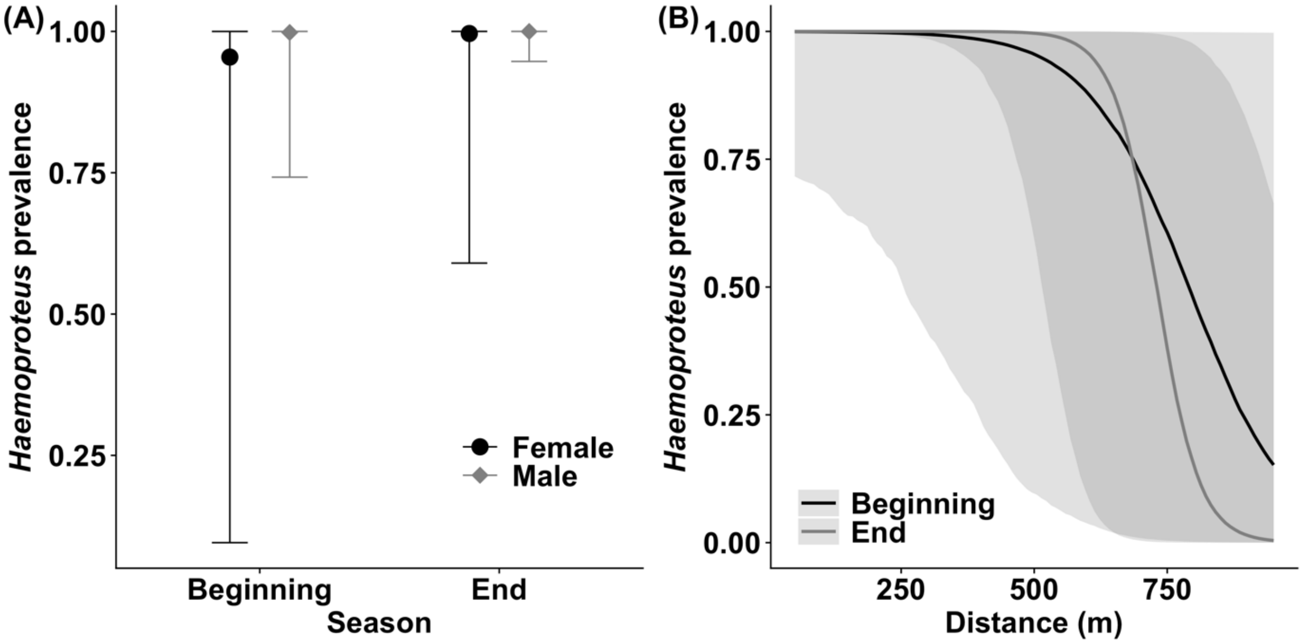

Figure 1. (**A**) *Haemoproteus* prevalence in the blood of male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (**B**) The association between the distance from the nearest water bodies and *Haemoproteus* prevalence at 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)).

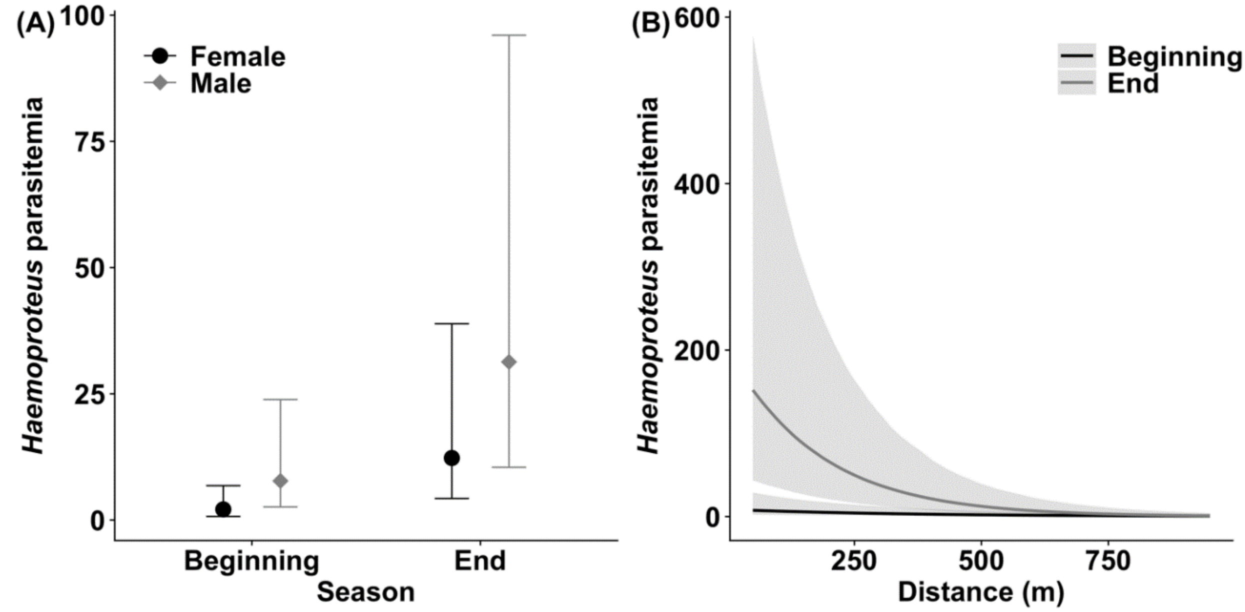

Figure 2. (**A**) *Haemoproteus* parasitemia in male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (**B**) The relationship between the *Haemoproteus* parasitemia and the distance to the nearest water bodies at the beginning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

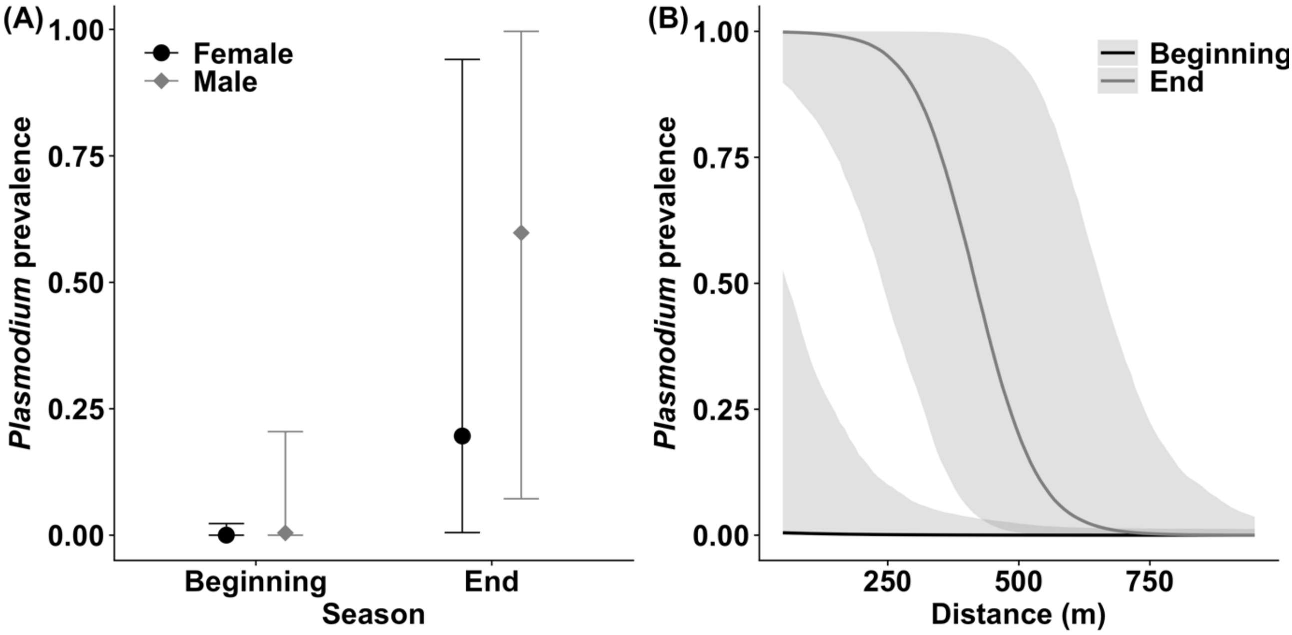

Figure 3. (**A**) *Plasmodium* prevalence in the blood of male and female Pied Flycatchers at the beginning and the end of the breeding season. Error bars represent 95% credibility intervals. (**B**) The relationship between the distance from the nearest water bodies and *Plasmodium* prevalence at the 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)).

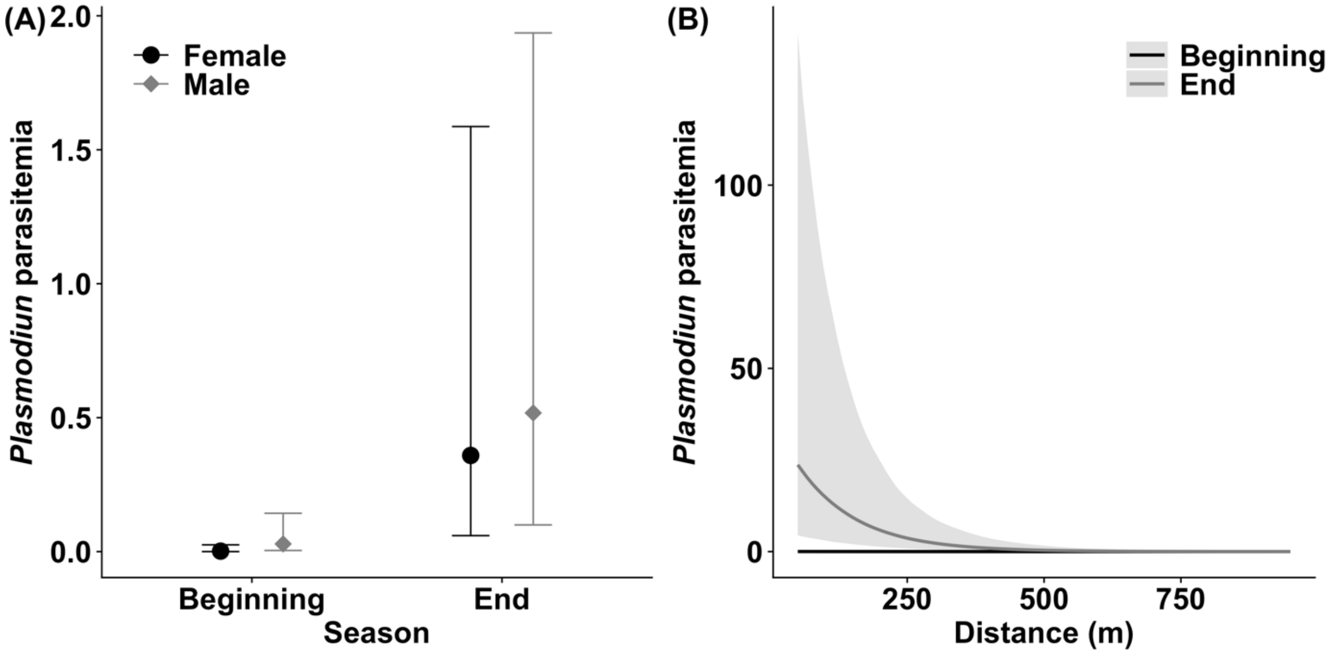

Figure 4. (**A**) *Plasmodium* parasitemia in male and female Pied Flycatchers at the beginning and end of the breeding season. Error bars represent 95% credibility intervals. (**B**) The relationship between *Plasmodium* parasitemia and the distance to the nearest water bodies at the beginning and end 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)).

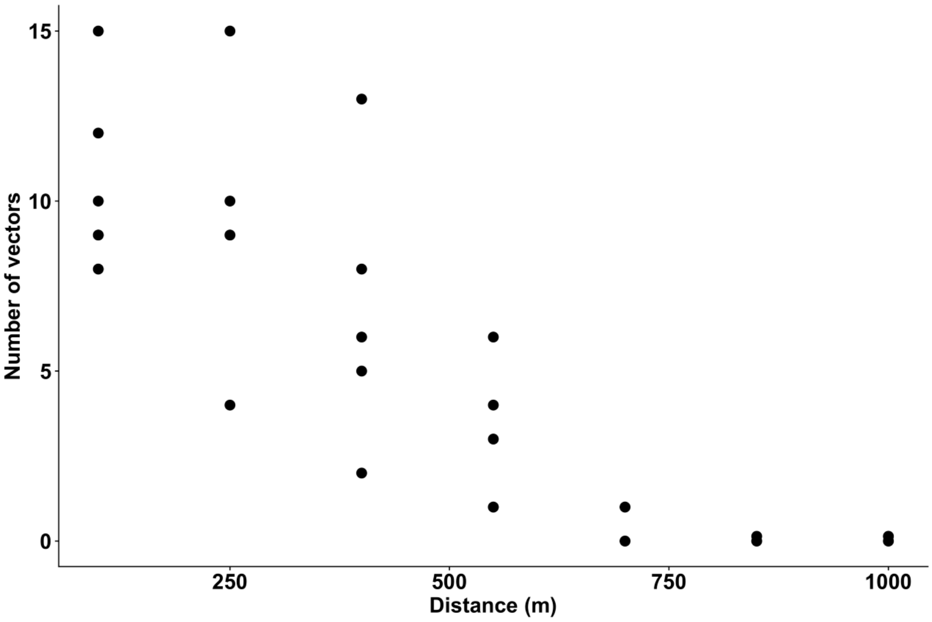

Figure 5. The relationship between the distance to the nearest forest water body and the number of parasite vectors trapped in nest boxes of Pied Flycatchers.

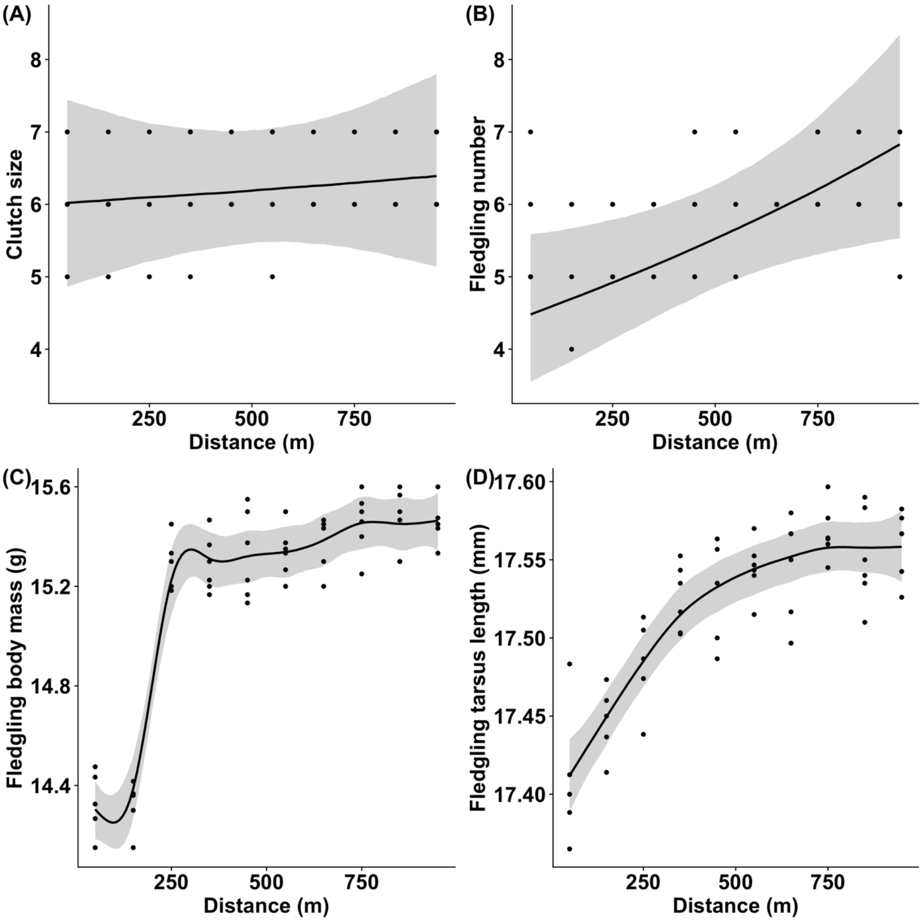

Figure 6. The relationships between the distance to the forest water bodies and clutch size (**A**), fledgling number (**B**), fledgling body mass (**C**), and fledgling tarsus length of Pied Flycatchers (**D**). Solid lines show the estimated trendlines by the model, and grey-shaded areas represent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

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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.

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

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III PUBLICATION

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ORIGINAL ARTICLE

Intensity of haemosporidian infection of parids positively correlates with proximity to water bodies, but negatively with host survival

Tatjana Krama[1] · **Ronalds Krams**[2] · **Dina Cīrule**[3] · **Fhionna R. Moore**[4] · **Markus J. Rantala**[5] · **Indrikis A. Krams**[6,7]

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Abstract In birds, haemosporidian parasites have been found to have direct pathogenic effects on the host with important consequences for their fitness. However, less is known about distribution patterns of parasite vectors, which may significantly affect parasite prevalence, infection intensity and, thus, pathogenicity in hosts. Here, we tested for relationships between infection intensity, survival, predation and distance from water bodies of mixed-species tit flocks. We found that the prevalence of *Haemoproteus* and *Plasmodium* infections decreased with increasing distance from forest lakes and bogs outside the bird breeding season. *Haemoproteus* and *Plasmodium* parasites were found to be associated with a low survival rate of willow tits (*Poecile montanus*) in the vicinity of water bodies, while crested tits (*Lophophanes cristatus*) were affected only by *Haemoproteus*. Crested tits, a dominant species of parid social groups, had a lower parasite prevalence and they survived better than the subordinate willow tit. This can be explained by the crested tits foraging higher in the pine canopy as parasite vectors supposedly cannot reach hosts in the upper canopy as equally as in lower parts of the canopy. We show that individuals staying in flocks further from the forest water bodies and spending more time foraging in the upper parts of the canopy have higher chances of survival into the next breeding season. This suggests that different forest and canopy areas may differ in terms of parasite risk and associated mortality. Finally, we found that the infection status of parids increases the probability of predation by the pygmy owl (*Glaucidium passerinum*). We conclude that distance from water bodies and foraging location in the forest canopy may affect the intensity of parasite infection with fitness consequences in wintering parids.

Keywords Blood parasites · Crested tit · Distance to water bodies · Non-reproductive season · Predation · Survival · Willow tit

Zusammenfassung

Die Intensität von Hämosporidieninfektionen bei Meisen korreliert positiv mit der Nähe zu Gewässern aber negativ mit dem Überleben des Wirts

Bei Vögeln ist gezeigt worden, dass Hämosporidien-Parasiten direkte pathogene Effekte auf den Wirt und wichtige Folgen für seine Fitness haben. Weniger ist jedoch über die Verbreitungsmuster der Parasitenvektoren bekannt, welche die Prävalenz, die Intensität der Infektion und somit die Pathogenität bei Wirten signifikant beeinflussen können.

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✉ Indrikis A. Krams
indrikis.krams@ut.ee

[1] Department of Plant Protection, Institute of Agricultural and Environmental Sciences, Estonian University of Life Science, 51014 Tartu, Estonia

[2] Department of Chemistry and Geography, University of Daugavpils, Daugavpils 5401, Latvia

[3] Institute of Food Safety, Animal Health and Environment BIOR, Riga, Latvia

[4] School of Psychology, University of Dundee, Dundee DD1 4HN, UK

[5] Department of Biology, Section of Ecology, University of Turku, 20014 Turku, Finland

[6] Institute of Ecology and Earth Sciences, University of Tartu, 51014 Tartu, Estonia

[7] Present Address: Department of Psychology, University of Tennessee, Knoxville, USA

Hier haben wir getestet, ob bei gemischten Meisenschwärmen Zusammenhänge zwischen Infektionsintensität, Überleben, Prädation und Entfernung zu Gewässern bestehen. Wir fanden, dass außerhalb der Brutsaison der Vögel die Prävalenz von *Haemoproteus*- und *Plasmodium*-Infektionen mit zunehmender Entfernung von Waldseen und Sümpfen abnahm. *Haemoproteus*- und *Plasmodium*-Parasiten waren mit niedrigen Überlebensraten von Weidenmeisen (*Poecile montanus*) in der Nähe von Gewässern assoziiert, während Haubenmeisen (*Lophophanes cristatus*) lediglich von *Haemoproteus* betroffen waren. Haubenmeisen, eine dominante Art in Meisen-Sozialgruppen, hatten geringere Parasiten-Prävalenz und überlebten besser als die rangniedrigeren Weidenmeisen. Dies kann damit erklärt werden, dass die Haubenmeisen weiter oben in den Kronen der Kiefern nach Nahrung suchten und Parasitenvektoren die Wirte weiter oben in der Krone vermutlich nicht so häufig erreichen können wie weiter unten in der Krone. Wir zeigen, dass Individuen, die sich in Schwärmen weiter entfernt von Waldgewässern aufhalten und mehr Zeit damit verbringen, weiter oben in der Krone nach Nahrung zu suchen, höhere Chancen haben, bis zur nächsten Brutsaison zu überleben. Dies deutet darauf hin, dass sich verschiedene Wald- und Kronenbereiche in Bezug auf das Parasitenrisiko und die damit verbundene Sterblichkeit unterscheiden. Schließlich fanden wir, dass der Infektionsstatus von Meisen die Wahrscheinlichkeit von Prädation durch den Sperlingskauz (*Glaucidium passerinum*) erhöht. Wir folgern, dass die Entfernung zu Gewässern und der Ort der Nahrungssuche in den Baumkronen die Intensität von Parasiteninfektionen bei überwinternden Meisen beeinflusst, was Folgen für ihre Fitness hat.

Introduction

Species abundance and distribution are currently the focus of intense ecological research (Dornelas et al. 2006; Ghosh-Harihar and Price 2014). Parasitism is considered to be one of the strongest forces shaping the community structure of host species through the effects on trophic interactions, food webs, competitive interactions and biodiversity (Svensson-Coelho and Ricklefs 2011; Schmid-Hempel 2011). The effects of parasitism can be particularly pronounced when the hosts are keystone species of an ecosystem.

Haemosporidians are obligate parasites that infect a wide range of vertebrates and use dipteran insects as vectors (Valkiūnas 2005). Infections of avian hosts with blood parasites belonging to the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* may have detrimental effects on host reproductive success and survival probability (Valkiūnas 1998; Merino et al. 2000; Valkiūnas and Iezhova 2004; Valkiūnas 2005; Stjernman et al. 2008; Palinauskas et al. 2009; Martínez-de la Puente et al. 2010; Knowles et al. 2010; Krams et al. 2013; de Jong et al. 2014). Parasite prevalence and infection intensity often depend on the host immune system and the outcome of an arms race between host immunity and the ability of parasites to invade their hosts (e.g., Krams et al. 2012a). However, vector prevalence and distribution may also have significant effects on an individual's risk of infection (e.g., Allander and Bennett 1994; Zhou et al. 2012; Krams et al. 2010, 2013; Martínez-De la Puente et al. 2011; Loiseau et al. 2012).

Avian haemosporidian parasites are not homogeneously distributed across their hosts' habitats and populations Lacorte et al. (2013). Blood parasites are often absent in the blood of birds in marine, saline arid or alpine/high altitude environments which can be explained by the absence or scarcity of parasite vectors (Warner 1968; van Riper et al. 1986; Bennett et al. 1992; Little and Earle 1995; Rytkönen et al. 1996; Piersma 1997; Stewart et al. 1997; Blanco et al. 1998; Figuerola 1999; Sol et al. 2000; Jovani et al. 2001; Valera et al. 2003; Atkinson et al. 2005; Hellgren et al. 2008; Krams et al. 2012a; Martínez-De la Puente et al. 2013). At high latitudes, the period of active transmission of blood parasites occurs during the summer season (van Riper 1991; Atkinson et al. 1988), while at low latitudes, it is associated with the rainy season (Young et al. 1993). Thus, proliferation of vector-borne parasitic diseases is linked not only to the immunity of hosts but also to the availability of suitable habitats for the vectors (e.g., Arriero et al. 2008; Arriero 2009; Sehgal 2010).

The *Plasmodium* parasites are transmitted by the representatives of a number of mosquito (*Culicidae*) species. *Haemoproteus* species are transmitted by mosquitoes, biting midges (*Culicoides*) and louse flies (*Hippoboscidae*) (Valkiūnas 2005; Kim et al. 2009; Ferraguti et al. 2013a, b). The *Leucocytozoon* species develop in biting midges and blackflies (*Simuliidae*) (Valkiūnas 2005). However, relatively little is known about the habitat preferences of the dipteran vectors that transmit avian blood parasites. It is certain that mosquitoes require standing water to reproduce, which increases the probability of *Plasmodium* infections in the vicinity of lakes and ponds (Kettle 1995; Ishtiaq et al. 2008; Njabo et al. 2009; Krams et al. 2010, 2012a, b) and slow rivers (Wood et al. 2007). Biting midges are found in fens, bogs, marshes, compost, mud and stream margins (Hendry 1989). Blackflies are found wherever there is permanent or semi-permanent running water, which is required for development during larval and pupal stages. Thus, the majority of vectors of bird blood parasites require wetlands to reproduce. Although this may increase the prevalence of blood parasites in some birds living near lakes, streams and bogs (e.g., Wood et al. 2007; Krams et al. 2010), the associations between parasite prevalence and habitat type of their hosts are not yet well understood.

The willow tit (*Poecile montanus*) and crested tit (*Lophophanes cristatus*) are keystone species of coniferous forests throughout temperate and subarctic Europe and, in the case of the willow tit, also of northern Asia (Snow and Perrins 1997). During the spring and early summer, adult willow tits and crested tits defend breeding territories and raise offspring. Soon after fledging, the young disperse from their natal grounds and join other territorial adults usually one to three territories away (Ekman 1989; Siffczyk et al. 2003). They form heterospecific flocks with non-kin willow and crested tits and other members of the Paridae guild (Ekman 1989). Crested tits and willow tits hoard food to survive in winter. These flocks remain stable in membership and space as members of flocks jointly defend their territory from other flocks from mid-summer till the next breeding season in early spring. Most studies of bird blood parasites have been conducted during the reproductive season of birds, when parasite vectors are predicted to be most abundant. However, some studies have also demonstrated high parasite prevalence outside the breeding season and even during the winter (Hauptmanová et al. 2002; Dunn et al. 2013, 2014), showing that birds may be at risk of infection in late summer and early autumn while parasite vectors remain active (e.g., Cheke et al. 1976; Rintamäki et al. 2000; Ishak et al. 2010; Kimura et al. 2010). The effects of blood parasite infections on their hosts outside the breeding season, however, have not yet been tested.

Here we investigated whether prevalence and infection intensity of blood parasites are related to the distance of territories of mixed-species tit flocks from forest lakes, streams and bogs where parasite vectors reproduce. We predicted a negative correlation between prevalence and intensity of infection and the distance of bird territories from water bodies, as is reported in human malaria (Midega et al. 2012). Some studies suggest that infection risk is highest some days or weeks after fledging (Valkiūnas 1993a, b), while other evidence shows that blood-sucking insects may attack nestlings (e.g., Caillouët et al. 2012, 2013; Krams et al. 2013). Willow and crested tits start their breeding season early in spring so that their nestlings are fully feathered or even fledged before the vectors of blood parasites emerge. Thus, it is likely that haemosporidians infect willow and crested tits during dispersal in the beginning of summer or later in the summer when they settle in their winter territories (Hauptmanová et al. 2002). We also checked whether haemosporidian infections of parids increase their probability of being predated upon by the pygmy owl (*Glaucidium passerinum*), the principal predator of passerine birds in northern Europe (Kullberg 1995; Kullberg and Ekman 2000).

Methods

Study site and birds

The study was conducted in the vicinity of Krāslava in southeastern Latvia in 2009 and 2012. The study area covers approximately 10 km^2 of coniferous forest plantations dominated by ca. 60–85-year-old Scots pines *Pinus sylvestris* (Rytkönen and Krams 2003). The study area is located on a plateau ca. 190 m above sea level. The area contains a few forest lakes, bogs, small streams and one large river with a number of bays suitable for mosquito reproduction. The majority of the area is dry pine forest on sandy soil with nearly no understory and does not contain any ditches or temporary water pools. The climate was similar across study years with ambient temperature above the average between August and the beginning of October. Mosquitoes and biting midges were abundant and actively flying throughout the study season (Spuris 1974; Spungis 2000).

The data were obtained from 20 mixed-species flocks containing 4–5 crested tits (mean number of individuals 4.30 ± 0.44, mean ± standard deviation (SD); 86 individuals in total) and 4–6 willow tits (mean number of individuals 4.10 ± 0.49, mean ± SD; 82 individuals in total). The birds were trapped by mist nets at temporary feeders baited with sunflower seeds. All flock members were captured in September. Willow tits and crested tits were sexed and aged (as adult or juvenile). The shape of the rectrices of willow and crested tits (Laaksonen and Lehikoinen 1976) and the color of the iris of crested tits (Bardin 1979; Lens and Dhondt 1992) were used to determine age. Sexual dimorphism in wing and tarsus length were used to sex individuals (Koivula and Orell 1988). Each bird was banded with metal and individual plastic rings.

Each mixed-species flock was followed for 18–24 h within 5–6 days to detect its boundaries using a Magellan GPS receiver (MiTAC Digital Corporation, Santa Clara, CA, USA). An observer recorded the flock's coordinates every five minutes (5 min) while following adult willow and crested tits. We determined the distance between the flock and the nearest water-body as the distance between the edge of the bog (all of the lakes were surrounded by bogs), stream or river and the closet point of the territory to the water-body visited by flock members. The distances were measured on a digital map.

Bird survival

We estimated the winter survival of the birds in the beginning of February. The birds that disappeared from the flocks but were found again as members of adjacent flocks, or as breeding birds in spring, were included in the analysis as survivors. We estimated the predation rate of willow tits and crested tits by counting the number of individuals in food caches of pygmy owls while checking nestboxes between October and January. We assume that all other birds not found were dead.

Blood parasites

At capture, blood samples (150 mg) were taken from the tarsal vein. For identification of 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 (Bennett 1970; Valkiūnas 2005).

Smears were screened with a light microscope under oil immersion at 1,000× magnification for *Haemoproteus* and *Plasmodium* and at 500× magnification for *Leucocytozoon*, *Trypanosoma* and *Microfilaria*. 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. Individuals were classified as infected when smears were positive for at least one hemoparasite taxon. The intensity of infection (parasitemia) was estimated as the number of parasite gametocytes per 10,000 erythrocytes (Valkiūnas 2005).

Statistics

The data on the prevalence of *Plasmodium* infection were not distributed normally in willow tits (one-sample Kolmogorov–Smirnov test), and we arcsine transformed the data to reach normality ($P = 0.052$). Total parasite prevalence was similar between 2009 and 2013 both in crested tits (Fisher's exact test, $P = 1$) and willow tits (Fisher's exact test, $P = 1$), so we pooled the data. In 2009 and 2013 we sampled birds from different flocks, hence each flock was treated as an independent data point. The total prevalence of haemosporidian parasites, prevalence of *Plasmodium* and prevalence of *Haemoproteus* were calculated for each flock. Since we did not detect any infection by *Leucocytozoon* whose vectors need streams to reproduce, we pooled all data from lakes, bogs and streams into a single category of forest water bodies. We used an individual bird as an independent data point when calculating the intensity of infection (parasitemia) and overwinter survival. We performed Fisher's exact tests with Bonferroni correction. All tests were two-tailed.

Results

Blood parasites

Crested tits were infected only by *Haemoproteus majoris*. Willow tits were infected with *Haemoproteus majoris* and *Plasmodium circumflexum*. We did not find any gametocytes of *Leucocytozoon*. No *Trypanosoma* and *Microfilaria* parasites were found in the samples of either crested or willow tits.

The parasitemias of crested tits infected by *Haemoproteus* (1.57 ± 4.24 gametocytes/10,000 erythrocytes) and willow tits infected by *Haemoproteus* (1.19 ± 2.80 gametocytes/10,000 erythrocytes) and *Plasmodium* (0.35 ± 0.72 gametocytes/10,000 erythrocytes) were low. We did not find any statistically significant differences in *Haemoproteus* parasitemias between infected willow tits and crested tits (one-way ANOVA, $F_{1,162} = 0.47$, $P = 0.50$). *Haemoproteus* parasitemia of crested tits did not vary significantly with distance from water bodies (one-way ANOVA, $F_{19,66} = 0.88$, $P = 0.61$). We did not find any significant variation of *Haemoproteus* (one-way ANOVA, $F_{19,63} = 1.23$, $P = 0.27$), while we found a significant variation in *Plasmodium* parasitemia (one-way ANOVA, $F_{19,63} = 4.07$, $P < 0.0001$) with distance from water bodies in willow tits.

Proportions of individuals within flocks infected with *Haemoproteus* in crested tits varied from 0 to 50 % (18.75 ± 19.25 %), and from 0 to 100 % in willow tits (32.50 ± 38.41 %). The prevalence of *Haemoproteus* significantly differed between crested tits (15 infected and 71 non-infected, prevalence 17.44 %) and willow tits (26 infected and 56 non-infected, prevalence 31.71 %; Fisher's exact test, $P = 0.047$). The proportion of individuals infected with *Plasmodium* varied between 0 and 100 % (23.75 ± 35.80 %) in willow tit flocks. *Plasmodium* prevalence of willow tits (19 infected and 63 non-infected, prevalence 23.17 %) and crested tits (all 86 non-infected and 0 infected prevalence 0 %) differed significantly as no *Plasmodium* infection was detected in crested tits (Fisher's exact test, $P = 0$). *Haemoproteus* and *Plasmodium* prevalences did not differ between adult (13 infected and 27 non-infected) and young willow tits (13 infected and 29 non-infected; Fisher's exact test, $P = 1$). Fifteen willow tits had mixed infections of *Haemoproteus* and *Plasmodium*.

Binary logistic regression (Nagelkerke's $R^2 = 0.272$, $P = 0.001$) revealed that proximity to water bodies increased the prevalence of *Haemoproteus* in crested tit flocks ($\beta = -0.005$, $P = 0.002$, Fig. 1), while age ($\beta = 0.27$, $P = 0.62$), sex ($\beta = -0.48$, $P = 0.39$), tarsus length ($\beta = 0.07$, $P = 0.67$), wing length ($\beta = 0.052$, $P = 0.71$) and body mass ($\beta = 0.09$, $P = 0.49$) did not

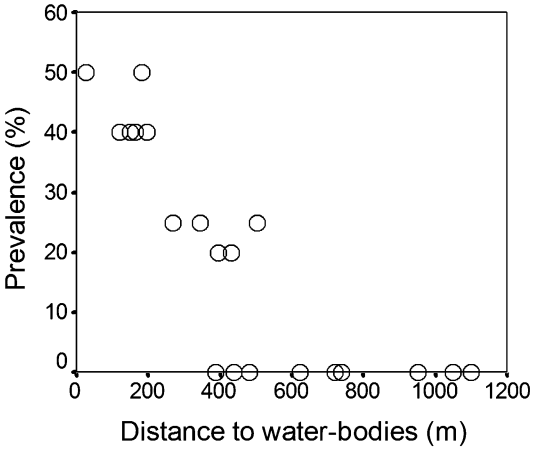

Fig. 1 Relationship between distance to the nearest water bodies and prevalence of *Haemoproteus* in crested tits

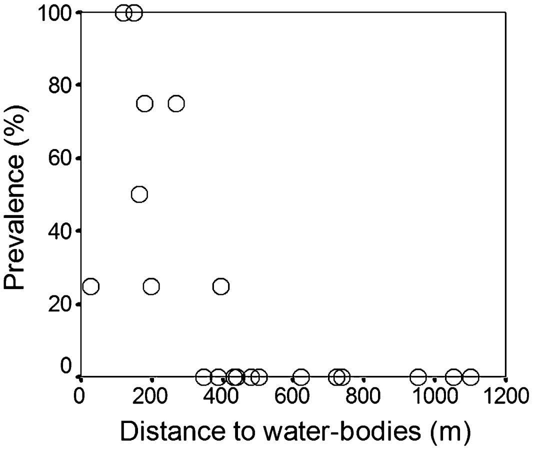

Fig. 3 Relationship between distance to the nearest water bodies and prevalence of *Plasmodium* in willow tits

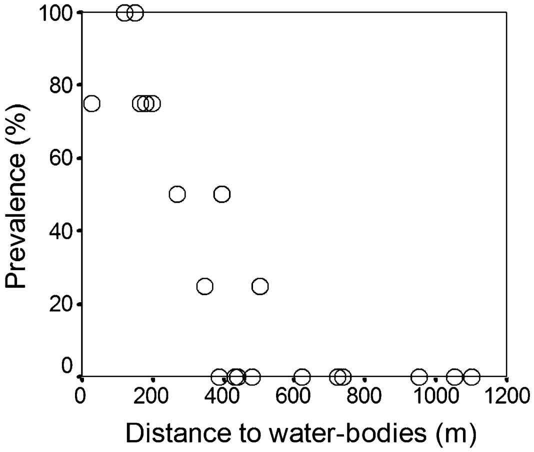

Fig. 2 Relationship between distance to the nearest water bodies and prevalence of *Haemoproteus* in willow tits

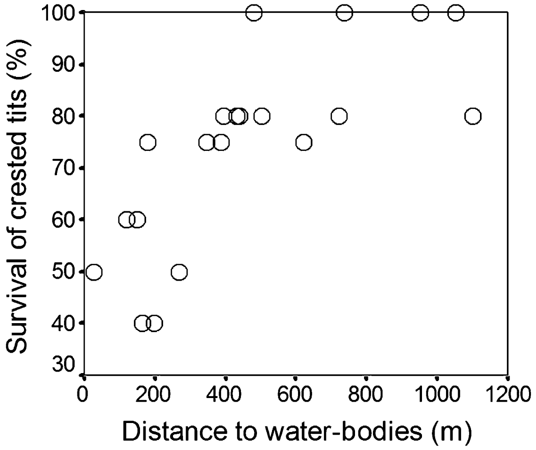

Fig. 4 Correlation between distance to the nearest water bodies and overwinter survival of crested tits

affect the prevalence of *Haemoproteus*. Binary logistic regression analysis (Nagelkerke's $R^2 = 0.543$, $P < 0.001$) showed that distance to water bodies was inversely related to *Haemoproteus* prevalence in flocks of willow tits ($\beta = -0.009$, $P < 0.0001$, Fig. 2), while age ($\beta = 0.22$, $P = 0.64$), sex ($\beta = 0.30$, $P = 0.53$), tarsus length ($\beta = 0.01$, $P = 0.69$), wing length ($\beta = 0.093$, $P = 0.44$) and body mass ($\beta = 0.50$, $P = 0.35$) did not affect parasite infection. Proximity to forest lakes increased the risk of *Plasmodium* infection in willow tits ($\beta = -0.01$, $P < 0.0001$, Fig. 3). The age of willow tits ($\beta = 0.60$, $P = 0.26$), sex ($\beta = -0.44$, $P = 0.40$), tarsus length ($\beta = 0.02$, $P = 0.59$), wing length ($\beta = -0.044$, $P = 0.74$) and body mass ($\beta = 0.10$, $P = 0.52$) did not contribute to *Plasmodium* infection (Nagelkerke's $R^2 = 0.589$, $P < 0.001$).

Survival in relation to water bodies

A total of 69 out of 86 (80.23 %) crested tits and 61 out of 83 (73.49 %) willow tits survived, which did not reveal any significant differences in survival rates between willow (22 found dead or disappeared) and crested tits (17 found dead or disappeared; Fisher's exact test, $P = 0.37$). Crested tit individuals that disappeared did not differ with respect to sex (Fisher's exact test, $P = 1.00$) nor did they do so with respect to survival in willow tits (Fisher's exact test, $P = 0.60$).

The proportion of crested tits in flocks that survived until the next breeding season significantly correlated with decreasing distance from the water bodies ($r = 0.74$, $n = 20$, $P < 0.0001$, Fig. 4). We found that survival of both adult crested tits ($r = 0.62$, $n = 20$, $P = 0.004$) and

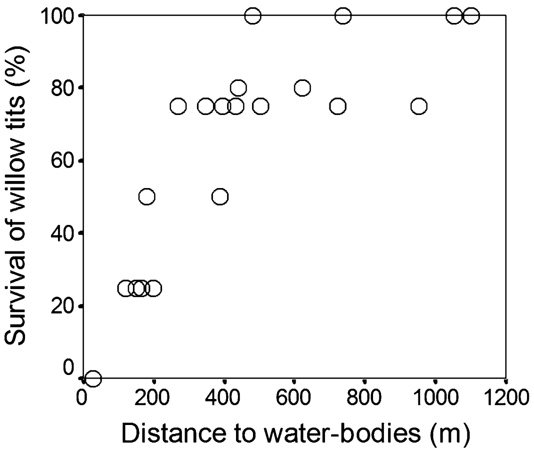

Fig. 5 Correlation between distance to the nearest water bodies and overwinter survival of willow tits

young individuals ($r = 0.75$, $n = 20$, $P < 0.0001$) increased away from water bodies. Willow tits also survived significantly better further from the lakes and bogs ($r = 0.79$, $n = 20$, $P < 0.0001$, Fig. 5). Both adult willow tits ($r = 0.58$, $n = 20$, $P = 0.008$) and young willow tits ($r = 0.83$, $n = 20$, $P < 0.0001$) survived significantly better away from the water bodies.

Infections

We found that un-infected crested tits survived (69 survived and 2 disappeared) significantly better than infected individuals (2 survived and 13 disappeared; Fisher's exact test, $P = 0.0001$). Non-infected willow tits also survived significantly better (54 survived and 2 disappeared) than willow tits infected (6 survived and 20 disappeared; Fisher's exact test, $P = 0.0001$).

Predation

We did not observe any dead parid in the forest except for 30 individuals found in caches of pygmy owls. We found 13 crested tits cached by pygmy owls and all of them were infected individuals (Fisher's exact test, $P = 0.044$). We also found 17 willow tits in caches of pygmy owls (16 infected vs. 1 un-infected; Fisher's exact test, $P = 0.022$), showing that pygmy owls mostly depredated infected willow and crested tits. In total, we found 74 bank voles (*Myodes glareolus*), 22 goldcrests (*Regulus regulus*), 16 coal tits (*Periparus ater*), 6 siskins (*Carduelis spinus*), 4 great tits (*Parus major*), 4 treecreepers (*Certhia familiaris*), 2 bullfinches (*Pyrrhula pyrrhula*) and the above-mentioned 17 willow tits and 13 crested tits in 25 caching sites of pygmy owls. The number of nestboxes used for caching food ($n = 12$ nestboxes used as caching sites near water bodies out of a total of 146 nestboxes vs. $n = 13$ out of a total of 168 nestboxes far from water bodies) and total number of cached birds/voles (38 birds/35 voles near water bodies, 46 birds/39 voles away from water bodies) did not differ between distances of 0–500 and 501–1,100 m away from water bodies (Fisher's exact tests, $P = 1.00$ and $P = 0.87$, respectively), suggesting that the intensity of bird predation was similar between locations near and further away from water bodies. According to observations of pygmy owl hunting behaviour and playbacks of their territorial calls, territories of wintering tit flocks were covered by home-ranges of eight territorial male pygmy owls.

Discussion

Some previous studies have already demonstrated a negative relationship between the distance from forest lakes and streams and the prevalence of haemosporidian parasites during the reproductive season of passerine birds (Wood et al. 2007; Krams et al. 2010, 2012b). This is the first evidence showing a similar relationship outside the reproductive season of birds, suggesting an overlooked issue affecting winter mortality in temperate passerines. Our study links the infection status of individual birds and their overwinter survival by showing that overwinter survival of members of mixed-species tit flocks is significantly lower in vicinities close to forest water bodies such as lakes and bogs.

Low ambient temperature, the reduced availability of food resources and respective increases of inter- and intraspecific competition for food and cover against attacking predators make satisfying the daily maintenance requirements of wintering crested tits and willow tits difficult. It has been recently shown that stress levels of wintering birds is positively related to the magnitude of the stressor, and generally winter stress is much higher than the stress experienced by breeding birds (Krams et al. 2011; Cīrule et al. 2012). This might be the main reason for the lower survival rates of the infected willow and crested tits compared to the non-infected individuals found in this study. However, further studies are needed to test whether infection status significantly increases levels of glucocorticoids or the heterophil and lymphocyte ratio (H/L ratio), two widely used methods to assess stress in animals. Dunn et al. (2013) found that yellowhammers (*Emberiza citrinella*) wintering in a climate milder than birds in our study showed significant changes in their H/L ratios, and an elevated white blood cell count when infected by *Haemoproteus* spp. compared to uninfected birds. Infected yellowhammers generally had shorter wings and lower overwintering survival. Another study revealed that yellowhammers may also be infected by *Leucocytozoon*, showing a relapse in late winter, possibly coincident with reduced food accessibility (Dunn et al. 2014).

The results of this study suggest that wintering territories located far from the water bodies may represent a safer environment in terms of pathogen risk, especially in willow tits. The probability of acquiring of an haemosporidian infection in both parid species in late summer and early autumn was much lower in areas distant from the forest lakes and bogs than in territories close to the water bodies. Noteworthy, the intensity of *Plasmodium* infection decreased further from water bodies in willow tits. Although we did not find any direct cost linked with disease incidence per se, the results of this study show that infected hosts incur severe mortality costs via predation. We demonstrate a positive association between infection and mortality by showing that infected willow and crested tits constitute a substantial part of the diet of wintering pygmy owls. Some studies have shown that diseased prey is easier to catch than healthy individuals and that predators will often consume infected prey (Friend 2002; Packer et al. 2003; Johnson et al. 2006; Duffy and Sivars-Becker 2007). This is probably because the infected individuals are less vigilant due to their seemingly elevated energy requirements under low ambient temperature. However, this needs to be tested experimentally. For example, it may be that infected tits carry lower under skin fat reserves. Further, because residual reproductive value is the average number of offspring that an individual is expected to produce after the current reproductive event, individuals with low residual reproductive value incur greater risks than other individuals. Therefore, individual willow and crested tits infected with blood parasites incur greater risks than those with no parasite infections. Some studies suggest (Møller and Nielsen 2007; Møller 2008) that the flight distances of birds decrease with the number of blood parasite species and the prevalence of blood parasites, meaning that infected individuals incur greater risks in terms of reduced flight distance and run elevated risks of mortality by predators that are allowed to approach potential prey.

Overwinter survival did not differ between adults and young individuals, and between sexes of crested and willow tits. However, we found a significantly lower prevalence of *Haemoproteus* infection in crested tits than in willow tits. Moreover, we did not find any *Plasmodium* infection in crested tits. A possible explanation would be a better immune response of crested tits against *Plasmodium* parasites as many bird species may have efficient immune responses against blood parasites (e.g., Krams et al. 2013).

Another explanation for the low prevalence of *Haemoproteus* and the lack of *Plasmodium* might be a rank-related distribution of members of tit groups within the tree canopy. Within mixed-species flocks of forest parids, a linear dominance hierarchy exists in which crested tits dominate willow tits, while males, with a few exceptions, dominate females and adults dominate juveniles (Ekman 1979; Hogstad 1987). Thus, age is a rough equivalent of social rank in wintering parids (Ekman 1989). It is noteworthy that the presence of dominant crested tits in wintering flocks is important in determining the fattening strategies of willow tits (Krams 1998), a crucial factor not only for wintering birds but also migrating birds. In the tree canopy, dominant crested tits prefer the upper parts, while subordinate willow tits are forced to forage in the lower canopy, a part of the tree that may be more exposed to attacks of parasite vectors. Although the abundance/presence of insect vectors was not quantified in this study, it was shown that numerous species of mosquitoes are recognized to preferentially inhabit tree canopies (Haddow et al. 1947; Main et al. 1966; Service 1971; Novak et al. 1981; Mitchell 1982; Reisen et al. 1990; Anderson et al. 2004; Savage et al. 2008). Vertical stratification is also influenced by humidity, temperature and light (Clements 1992), which may make crested tits foraging in the upper canopy less vulnerable to mosquito attacks than willow tits in the middle or lower canopy (Černý et al. 2011). Moreover, it has been shown that midges prefer to bite near the ground and are uncommon at heights more than about 3 m from the ground (Mitchell 1982), making these parasite vectors less important to dominant individuals high in the canopy. It is important to note that initiation of host-seeking activity in mosquitoes is usually associated with the end of civil twilight and activity is supposed to occur over an extended nighttime period in the southern latitudes (Savage et al. 2008). However, the summer nights are too short at high latitudes in northern Europe, and mosquitoes may attack their hosts at any time of the day except for in the direct sunlight. The biting midge is usually most active in the two hours before sunset with less activity after dark. Most midge attacks, therefore, occur around dusk, although midges can also be active on cloudy days and in shaded areas (Mitchell 1982; Černý et al. 2011). This suggests that parids can be attacked by their dipteran vectors not only at night but also during their foraging activities (personal observation).

The results of this field study show that overwinter survival of members of mixed-species flocks of parids depend not only on the availability of food, the presence of predators, and dominance rank (Krams 1998; Krams et al. 2001), but also on parasite infections and proximity to areas where parasite vectors reproduce. We show a lower prevalence of blood parasites in dominant members of mixed-species tit flocks foraging in the upper parts of the canopy (Krams 2001). It indicates that some forest and canopy parts may be less accessible to parasite vectors and more preferable to birds (Ekman 1987; Krama et al. 2008), while areas close to the forest lakes and other water bodies might become ecological traps for breeding and wintering birds. We suggest that foraging and perhaps nesting and singing in higher parts of the canopy might be beneficial in terms of lower parasitism and higher survival because of supposedly lower densities of blood parasite vectors there. Overall, our study shows the importance of linking the research on spatial distribution and life history of hosts and the distribution of vectors of their haemosporidian parasites (Valkiūnas 2011; Oakgrove et al. 2014). Finally, the effect of predation on the distribution of parasites and virulence evolution is addressed in a few studies. Choo et al. (2003) and Morozov and Adamson (2011) suggested that adding predators into host–parasite systems can result in evolutionary suicide in the parasite. The results of this study support this theoretical idea. As an explanation for the rarity of relapses in chronically infected individuals during the next breeding season, we suggest that most infected hosts are depredated during wintering season. Future correlational and experimental studies are required to reveal the impact of predation on the resulting outcome of virulence evolution and its epidemiological consequences in detail.

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