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Weather impacts on interactions between nesting birds, nest-dwelling ectoparasites and ants

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Weather has a dominant impact on organisms, including their life histories and interspecific interactions. Yet, for nesting birds, and the arthropods inhabiting bird nests, the direct and cascading effects of weather are poorly known. We explored the influence of ambient temperatures and rainfall on the cohabitation of dome-shaped bird nests by Wood Warblers *Phylloscopus sibilatrix*, their blowfly *Protocalliphora azurea* ectoparasites, and predatory *Myrmica* and *Lasius* ants that may provide nest sanitation. We sampled blowflies and ants in 129 nests, and measured warbler nestlings during 2018–2020 in the primeval Białowieża Forest, eastern Poland. The probability of ectoparasites occurring in nests increased with increasing ambient temperatures and declining precipitation in the early nestling stage, when adult blowflies are ovipositing. Where present, the number of ectoparasites was greater if higher ambient temperatures had prevailed in the late nestling stage, but only when ants were absent from nests. However, the nestling growth was unrelated to ectoparasite abundance or ant presence within bird nests, although it was lower at high rainfall. The results suggest that weather can have conflicting impacts on interactions between nesting birds and nest-dwelling arthropods, but birds can mostly compensate for any related costs in old-growth forest, where food is generally abundant.

Climate and weather have intricate effects on organisms, with direct implications for their life histories, abundance and distributions, but also reciprocal indirect effects via interspecific interactions^{1–3}. As individual species vary in their requirements and tolerance to weather, any variation in ambient conditions may cause divergent responses that affect interspecific interactions^{4,5}. Due to the complexity of interaction networks between organisms⁶, predicting the directions and outcomes of changes in weather can be challenging, yet is crucial in the face of climate change and shifting weather patterns³.

Weather is known to have potential cascading effects via ecological links between species within broad habitats and, in extreme situations, to cause significant shifts of ecosystem functioning. Such examples from different types of ecological networks include food webs, mutualistic relationships and host-parasite networks^{2,3,7,8}. However, similar analyses are scarce for microenvironments, such as bird or mammal nests, which may host a diversity of interconnected species, and function as ‘microecosystems’.

The nests of endothermic birds and mammals are inhabited by a rich fauna of arthropods, comprising predators, scavengers and ectoparasites^{9,10}. These communities may form complex ecological networks within nests, and also interact with the hosts^{9,11,12}. Although bird and mammal nests are composed of insulative materials to buffer the owners against ambient conditions^{12,13}, weather might still influence the hosts and the arthropod community within the nests. Therefore, as with impacts on species in broad habitats, the cascading effects of weather (e.g. ambient temperatures or rainfall) may also affect coexisting species on this smaller scale within the microenvironment of a nest.

The arthropods inhabiting bird nests are relatively well studied, and most research has focused on relationships between nesting birds and nest-dwelling ectoparasites, such as blowflies *Protocalliphora* spp. (Diptera: Calliphoridae) (89 papers published since 1977 according to Web of Science accessed on 23 February 2022; key words: (“bird” OR “nest”) AND “blowfly”). Blowfly larvae or pupae have been recorded in the nests of hundreds of bird species across the Holarctic¹⁴, but systematic studies of blowfly infestation come almost exclusively from

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cup-shaped nests built inside cavities, mainly nest-boxes. Similar research is generally lacking for songbirds that build dome-shaped nests which are unenclosed within a tree or rock cavity, and so are directly exposed to ambient conditions.

The few studies comparing nest microclimates indicate that the insulation of dome-shaped nests is similar to unenclosed, open-cup nests^{15–17}, contradicting assumptions of a more stable microclimate in the former^{18–20}. For example, measurements of the dome-shaped nests of Wood Warblers *Phylloscopus sibilatrix* showed large daily temperature fluctuations within the nest walls (mean daily internal amplitudes ranging between 4 and 13 °C, at mean daily ambient amplitudes of 6–16 °C), with internal temperatures that strongly depended on ambient conditions²¹. Thus, the hosts and the arthropods inhabiting unenclosed, dome-shaped nests could be greatly exposed to variable weather, despite some protection provided by the roof against direct solar radiation or rainfall. Nevertheless, more studies on the microclimate of dome-shaped nests are necessary to assess their thermal and humidity properties in comparison to unenclosed, open-cup nests.

It has been suggested that nest infestation by blowflies could be hindered by cool and wet weather^{22–24}. Low ambient temperatures and heavy rainfall might reduce the activity of adult blowflies ovipositing in bird nests^{25–27}, presumably resulting in fewer nests being parasitised. Despite the thermal activity of birds within their nests^{21,28}, cool weather might also negatively affect the nest microclimate for developing blowfly larvae. The period of blowfly larvae development may be shortest at nest temperatures of c. 35 °C²⁷, while lower nest temperatures (e.g. 13–18 °C) would extend the larval stage²⁷, and potentially reduce ectoparasite numbers in cooler nests²⁹. As such, cool and wet weather might limit blowfly nest infestation and the negative impact of ectoparasites on hosts^{29,30}. Other reasons for varying nest infestation by blowflies may include the brood size of hosts, variation between habitats, and/or other undefined factors related to annual and within-season variation^{24,26,29,31–33}. Nest sanitation by birds actively searching for ectoparasites in the nesting material may also be important³⁴.

As bird nests are inhabited by communities of nest-dwelling arthropods⁹, weather might also influence ectoparasite infestation indirectly, via potential predator–prey interactions. For example, ants can act as predators and reduce the number of nest-dwelling ectoparasites, such as bugs *Oeciacus vicarius* (Heteroptera: Cimicidae) or flies *Carnus hemapterus* (Diptera: Carnidae)^{35,36}. As the foraging activity of ant workers can be promoted by warm weather^{37,38}, the sanitation of bird nests by ants might be more effective at higher ambient temperatures, potentially having subsequent fitness consequences for the host birds.

Warm and dry weather may also have a positive influence on the host birds by, for example, increasing the availability of food and promoting the growth or survival of nestlings^{39–41}. However, this benefit might be limited by the increased ectoparasite (blowfly) infestation of bird nests during warm and dry weather, although this, in turn, might then be mitigated by increased foraging by predatory ants (see above). Other factors, such as habitat type, brood size or nestling age, might moderate the influence on birds of the ambient conditions, ectoparasites or ants^{40,42–45}. Therefore, a holistic approach is needed to unravel the intricacy of host responses and interspecific interactions to convoluted weather effects within the microenvironments of bird nests.

In this study, we investigated the influence of weather on interactions between nesting Wood Warblers (song-bird hosts), blowflies *Protocalliphora azurea* (Fallén, 1817; ectoparasites), and *Lasius* or *Myrmica* ants (predators of arthropods), which all cohabit in the birds' dome-shaped nests. First, we assessed the occurrence and intensity of blowfly infestation in the bird nests. We then tested whether the ectoparasite infestation varied with changing ambient temperatures and rainfall in the early nestling period, when chicks were young and female adult blowflies would be ovipositing in the bird nests²⁷. We repeated these tests for the late nestling period, when chicks were older and the blowfly larvae would be developing within bird nests¹⁴. Additionally, we checked whether reduced occurrence or intensity of ectoparasite infestation was associated with the presence of ants at a range of ambient conditions, when the foraging activity of ant workers may vary^{37,38}. We also explored the fitness consequences for birds, expressed as the variation in the growth (feather length and body mass) in relation to weather, blowfly parasitism, or ant presence within the nests. Co-variables of habitat type, study year, bird nest phenology, brood size and nestling age were considered in explaining the degree of blowfly infestation or nestling growth, hypothetically moderating the observed patterns. Finally, we compared the mortality of nestlings (brood reduction between nestlings hatching and leaving the nests) in the nests with and without blowflies.

Results

The occurrence and intensity of ectoparasite infestation. Blowflies were the near-exclusive nest-dwelling ectoparasites in the Wood Warbler nests in the Białowieża National Park, eastern Poland. Only one nest contained a single flea (Siphonaptera), and in ten nests we found single ticks (Ixodidae).

The occurrence of blowflies was generally low, being recorded in 17 of 49 nests in 2018, seven of 26 nests in 2019, and six of 54 nests in 2020. The number of blowflies per infested nest averaged 29.6 (95% CIs: 21.3–38.1, range: 1–63, $n = 17$ nests) in 2018, 32.0 (95% CIs: 11.7–57.9, range: 3–97, $n = 7$) in 2019 and 33.7 (95% CIs: 26.8–44.0, range: 24–58, $n = 6$) in 2020.

The occurrence and intensity of blowfly infestation varied with weather, but the relationship differed depending on ambient conditions in the early or late nestling stage. In the early nestling stage, when nestlings were 1–4 days old, the likelihood of blowfly presence increased with the mean ambient temperature and decreasing sum of rainfall (Fig. 1a,b; Tables 1, 2). However, in the late nestling stage, the relationship between the occurrence of blowflies and weather conditions was weak; only the sum of rainfall was retained in the binomial part of hurdle models with $\Delta\text{AICc} < 2$ (Table 1), but became insignificant in averaged models (Table 2).

When mean ambient temperature in the late nestling stage was dropped from the hurdle binomial models with $\Delta\text{AICc} < 2$ (Table 1), the likelihood of blowfly presence appeared lowest in 2020, and generally increased in broods initiated later in a season (Table 2). The likelihood of blowfly presence was weakly related to other factors, such as ant presence (lone foraging workers and any associated larvae or pupae), Wood Warbler brood

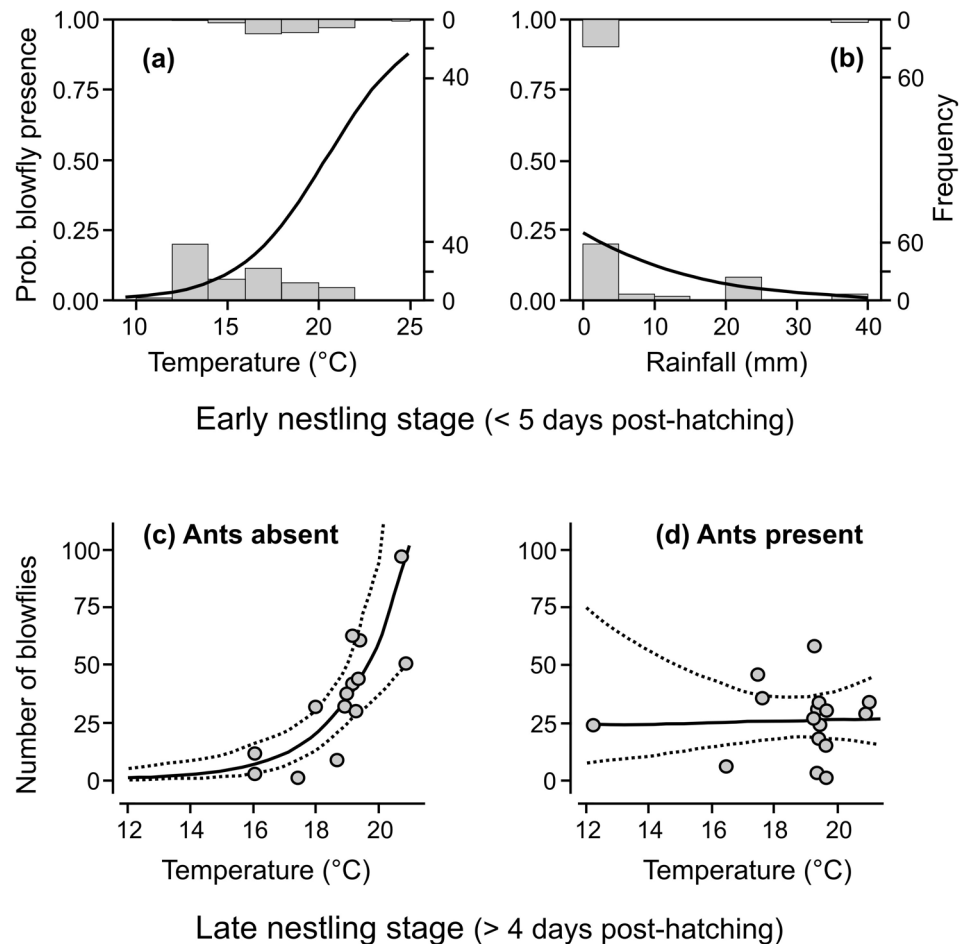


Figure 1. The likelihood of blowfly *Protocalliphora azurea* presence in relation to weather, (a) mean ambient temperature and (b) total sum of rainfall, in the early nestling stage of Wood Warblers *Phylloscopus sibilatrix* ($n = 129$ nests). Additionally, changes in blowfly number in parasitised nests with increasing mean ambient temperature in the late nestling stage: (c) nests without ants ($n = 14$ nests) and (d) nests with ants ($n = 16$ nests). Solid lines represent trends, and dashed lines are 95% confidence intervals (CIs) of hurdle models with $\Delta\text{AICc} = 0.00$ (Table 1; package `pscl`^{92,93}). Shown are histograms of the number (frequency) of nests containing blowflies (upper) and those without blowflies (bottom) (grey bars in panel a and b).

size, or habitat type; the variables were excluded from the top models ($\Delta\text{AICc} < 2$) or became insignificant in the binomial part of averaged models (Tables 1, 2).

The number of blowflies in infested nests seemed unrelated to weather conditions in the early nestling stage, as both weather variables were excluded from the count part of models with $\Delta\text{AICc} < 2$ (Table 1). Notably, blowflies were more numerous in parasitised nests when exposed to higher mean ambient temperatures in the late nestling stage, but only if ants were absent (Fig. 1c). When ants were present in the same nests, the intensity of blowfly infestation remained mostly unchanged at the range of ambient temperatures (Fig. 1d). The two-way interaction term between ant presence and ambient temperature in the late nestling stage was significant in the count part of averaged models with $\Delta\text{AICc} < 2$ (Tables 1, 2). The total sum of rainfall in the late nestling stage was dropped from the count part of models with $\Delta\text{AICc} < 2$, indicating a weak relationship with the number of blowflies in parasitised nests (Table 1). Overall, the intensity of blowfly infestation tended to be lower in nests containing ants, averaging 26.0 blowfly larvae or pupae (95% CIs: 18.8–33.2, $n = 16$ nests), compared to a mean of 36.8 (95% CIs: 24.0–50.6, $n = 14$) in nests without ants.

The number of blowflies in infested nests tended to be higher in broods initiated later in a season (Tables 1, 2). However, the relationship became significant only when the mean ambient temperature in the early nestling stage was dropped from the count part of models with $\Delta\text{AICc} < 2$ (Tables 1, 2). There was little variation in the intensity of blowfly infestation in relation to study year, habitat type, or brood size, as these variables were dropped from the count part of models with $\Delta\text{AICc} < 2$, or became insignificant if retained (Tables 1, 2).

The growth of Wood Warbler nestlings. The length of nestling primary feathers tended to be shorter with an increasing total amount of rainfall during the period from when the nestlings were 5 days old and until they were measured at a median 8 days old (Fig. 2a; Tables 3, 4). There was an insignificant relationship between

Model (count binomial part)	df	Log(L) ^b	AICc	ΔAICc	Weights
Weather in early nestling stage (nestlings < 5 days old)					
Hatching date ^a temperature ^b + rain ^c	6	-183.7	380.1	0.00	0.015
Hatching date temperature + rain + brood size ^d	7	-182.9	380.7	0.61	0.011
Habitat type ^e temperature + rain	6	-184.4	381.5	1.36	0.008
Hatching date temperature + rain + ants ^f	7	-183.3	381.5	1.42	0.008
Hatching date + habitat temperature + rain	7	-183.4	381.6	1.52	0.007
Hatching date temperature + rain + habitat	7	-183.4	381.7	1.58	0.007
Hatching date temperature + rain + ants + brood size	8	-182.3	381.8	1.73	0.007
Hatching date + ants temperature + rain	7	-183.5	382.0	1.92	0.006
Habitat temperature + rain + brood size	7	-183.6	382.1	1.97	0.006
Weather in late nestling stage (nestlings > 4 days old)					
Temperature + ants + temp. × ants year ^g + hatching date + rain	10	-181.4	384.6	0.00	0.080
Temperature + ants + temp. × ants year + hatching date	9	-183.4	386.3	1.67	0.035
Temperature + ants + temp. × ants + brood size year + hatching date	10	-182.3	386.4	1.83	0.032

Table 1. Selection of hurdle negative binomial models ($\Delta\text{AICc} < 2$) testing blowfly *Protocalliphora azurea* infestation of 129 Wood Warbler *Phylloscopus sibilatrix* nests (response variable) depending on weather in early or late nestling stages. The count part with negative binomial distribution estimated changes in the number of blowflies in infested nests, and the hurdle binomial tested the likelihood of blowfly presence (package `pscl`^{92,93}). A null model had only fixed intercepts on the count and binomial parts. ^aRelative hatching date of nestlings (days from the median hatching date in a year); ^ban average of daily means (°C); ^ca sum of daily sums (mm); ^dthe number of nestlings hatched; ^ehabitat type (deciduous or mixed deciduous-coniferous); ^fpresence or absence of ants in bird nests (as a factor); ^gstudy year (2018–2020; as a factor); ^hlog-likelihood.

Variable	Weather in early nestling stage				Weather in late nestling stage			
	estimate	s.e.m	z	95% CI	estimate	s.e.m	z	95% CI
Count part with negative binomial distribution								
Intercept	3.34	0.34	9.7	2.67, 4.02	-6.64	2.82	2.4	-12.16, -1.11
Temperature	NA	NA	NA	NA	0.56	0.14	3.9	0.28, 0.84
Ants (present)	-0.17	0.29	0.6	-0.74, 0.41	10.21	3.14	3.2	4.05, 16.38
Temp. × ants (present)	NA	NA	NA	NA	-0.55	0.17	3.3	-0.88, -0.23
Hatching date	0.05	0.02	2.0	0.00, 0.09	NA	NA	NA	NA
Habitat (deciduous)	-0.50	0.38	1.3	-1.25, 0.24	NA	NA	NA	NA
Brood size	NA	NA	NA	NA	-0.32	0.22	1.5	-0.74, 0.11
Log(theta)	0.57	0.30	1.9	-0.02, 1.17	0.93	0.31	3.0	0.31, 1.55
Binomial (hurdle) part								
Intercept	-8.91	2.87	3.1	-14.55, -3.28	-0.87	0.33	2.6	-1.52, -0.22
Temperature	0.43	0.12	3.7	0.20, 0.65	NA	NA	NA	NA
Rain	-0.08	0.03	2.4	-0.14, -0.01	0.06	0.03	1.9	0.00, 0.12
Year (2019)	NA	NA	NA	NA	-0.67	0.60	1.1	-1.84, 0.50
Year (2020)	NA	NA	NA	NA	-2.57	1.08	2.4	-4.69, -0.45
Hatching date	NA	NA	NA	NA	0.19	0.06	3.2	0.08, 0.30
Ants (present)	0.48	0.49	1.0	-0.49, 1.44	NA	NA	NA	NA
Habitat (deciduous)	-0.55	0.67	0.8	-1.87, 0.77	NA	NA	NA	NA
Brood size	0.43	0.34	1.3	-0.23, 1.10	NA	NA	NA	NA

Table 2. Model-averaged covariates best explaining the number of blowflies in infested nests of Wood Warblers (count), and the likelihood of blowfly presence (binomial) in nests (package `pscl`^{92,93}). Shown are (conditional) model-averaged coefficients and confidence intervals (CI) across top models ($\Delta\text{AICc} < 2$) with different sets of covariates on count and binomial parts (Table 1). Significant relationships ($P < 0.05$) are marked in bold; NAs—covariates dropped during model selection (present in models with $\Delta\text{AICc} \geq 2$).

feather length and mean ambient temperature in the same period, as the temperature was dropped from the top linear mixed effects models with $\Delta\text{AICc} < 2$ (Table 3). The body mass of nestlings changed little in relation to ambient temperatures and rainfall during the period from when they were 5 days old and until they were measured (both weather variables were insignificant in averaged models; Tables 5, 6).

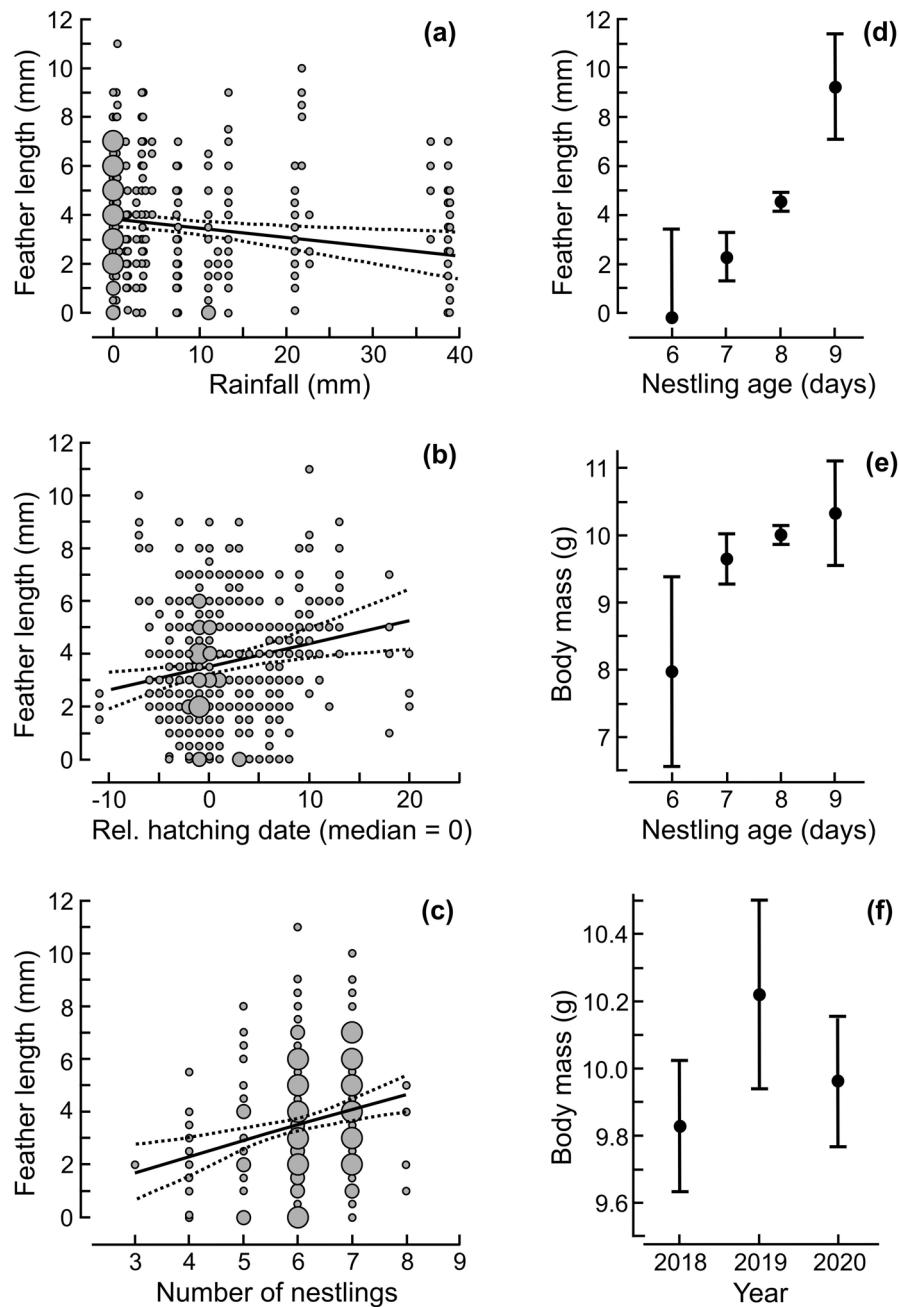


Figure 2. The length of the 3rd primary feather or body mass of Wood Warbler nestlings in relation to (a) the total sum of rainfall in the period when nestlings were > 4 days old until their measurement at median 8 days old; (b) relative hatching date (days from median hatching date in a year), (c) brood size (number of nestlings per nest), (d–e) nestling age since hatching, and (f) year. Solid lines indicate trends (a–c), black dots are means (d–f), and dashed lines or whiskers are the 95% CIs from the models with $\Delta\text{AICc}=0.00$ (Tables 3 and 5). The size of grey dots indicates sample sizes: small (1–10 nestlings measured), medium (11–20), large (> 20 nestlings). In total, 742 nestlings were measured from 129 nests in 2018–2020.

The growth of Wood Warbler nestlings was weakly related to blowfly abundance, i.e. the number of ectoparasites per nestling in all 129 nests with and without blowflies. Although some of the models that best explained the change in length of primary feathers or body mass of nestlings did include blowfly abundance (Tables 3 and 5), this variable was insignificant in averaged models (Tables 4 and 6). The nestling growth (feather length and body mass) appeared similar between nests that contained ants and those without (the variable was dropped from models with $\Delta\text{AICc} < 2$; Tables 3 and 5).

The length of the primary feathers was greater in older nestlings from larger broods that were raised later in the spring (Fig. 2b–d; Tables 3, 4). The body mass of nestlings showed a strong increase only with their age and was greatest in 2019 (Fig. 2e–f; Tables 5, 6). Nestling growth was similar in deciduous and mixed

Models	df	Log(L) ^f	AICc	ΔAICc	Weights
Rain ^a + hatching date ^b + brood size ^c + nestling age ^d	9	-1389.7	2797.5	0.00	0.204
Blowfly abundance ^e + rain + hatching date + brood size + nestling age	10	-1389.6	2799.5	1.91	0.079

Table 3. Selection of linear mixed effect models ($\Delta\text{AICc} < 2$) best explaining variation in the length of the 3rd primary feather (mm) of Wood Warbler nestlings (response variable; $n = 129$ nests). The remaining covariates also included in the global model, but dropped during model selection, were: the average mean daily ambient temperature ($^{\circ}\text{C}$) in the period when nestlings were > 4 days old until their measurement (at median 8 days old), ant presence (as a factor), habitat type (deciduous or mixed deciduous-coniferous) and study year (as a factor). A null model had only a fixed intercept, and a random effect was the individual nest. ^aThe total sum of rainfall (mm) in the nestling stage when nestlings were > 4 days old until their measurement; ^brelative hatching date of Wood Warbler nestlings (days from the median hatching date in a year); ^cthe number of nestlings hatched; ^dthe number of days since hatching (day 0; set as a factor); ^ethe number of blowfly larvae or pupae per nestling in nests with and without blowflies; ^flog-likelihood.

Variables	Estimate	s.e.m	z	CI 2.5%	CI 97.5%
Intercept	-3.81	1.86	2.0	-7.461	-0.160
Blowfly abundance	0.02	0.06	0.4	-0.093	0.137
Rain	-0.04	0.01	2.7	-0.064	-0.010
Hatching date	0.09	0.03	2.8	0.027	0.148
Brood size	0.59	0.17	3.5	0.262	0.920
Nestling age					
7 days	2.16	1.61	1.3	-1.012	5.331
8 days	4.04	1.57	2.6	0.951	7.131
9 days	7.94	1.83	4.3	4.356	11.529

Table 4. Model-averaged variables best explaining the length of the 3rd primary feather (mm) of Wood Warbler nestlings (response variable). Shown are averaged coefficients and confidence intervals (CI) across models with $\Delta\text{AICc} < 2$ (Table 3; conditional average). Significant relationships ($P < 0.05$) are marked in bold. For the description of variables see Table 3.

Models	df	Log(L)	AICc	ΔAICc	weights
Year + nestling age	8	-907.3	1830.8	0.00	0.034
Temperature + nestling age	7	-908.3	1830.8	0.06	0.033
Temperature + year + nestling age	9	-906.5	1831.2	0.38	0.028
Nestling age	6	-909.8	1831.7	0.90	0.022
Year + hatching date + nestling age	9	-906.9	1832.0	1.27	0.018
Year + hatching date + brood size	9	-907.1	1832.4	1.63	0.015
Rain + year + nestling age	9	-907.1	1832.4	1.64	0.015
Temperature + brood size + nestling age	8	-908.1	1832.4	1.65	0.015
Temperature + rain + nestling age	8	-908.3	1832.7	1.92	0.013
Year + nestling age + habitat type	9	-907.2	1832.7	1.96	0.013
Blowfly abundance + year + nestling age	9	-907.3	1832.7	1.97	0.013
Blowfly abundance + temperature + nestling age	8	-908.3	1832.8	1.99	0.013
Temperature + hatching date + nestling age	8	-908.3	1832.8	2.00	0.013

Table 5. Selection of linear mixed effect models ($\Delta\text{AICc} < 2$) best explaining the variation in body mass (g) of 742 Wood Warbler nestlings from 129 nests (response variable). The remaining covariate also included in the global model, but dropped during model selection, was ant presence (as a factor). A null model had only a fixed intercept, and a random effect was the nest identity. For the description of covariates see Table 3.

deciduous-coniferous stands, as habitat type was excluded from the models with $\Delta\text{AICc} < 2$ (Table 3) or became insignificant in averaged models (Tables 5–6).

Mortality of Wood Warbler nestlings. Wood Warbler brood reduction (i.e. nestling mortality) from hatching to fledging was uncommon, occurring in 11 of 86 successful nests in total (two of 35 successful nests in 2018, four of 16 nests in 2019, and five of 35 in 2020). The difference between the number of nestlings fledged

Variables	Estimate	s.e.m	z	CI 2.5%	CI 97.5%
Intercept	8.21	0.87	9.4	6.499	9.925
Blowfly abundance	0.00	0.03	0.0	-0.049	0.050
Temperature	-0.03	0.02	1.6	-0.070	0.008
Rain	0.00	0.01	0.5	-0.018	0.010
Year (2019)	0.38	0.18	2.1	0.030	0.731
Year (2020)	0.11	0.16	0.7	-0.196	0.425
Hatching date	0.00	0.02	0.3	-0.038	0.029
Brood size	-0.05	0.08	0.7	-0.203	0.100
Nestling age					
7 days	1.70	0.74	2.3	0.241	3.161
8 days	2.01	0.72	2.8	0.590	3.425
9 days	2.28	0.83	2.7	0.652	3.914
Habitat type (deciduous)	0.06	0.19	0.3	-0.307	0.421

Table 6. Model-averaged variables best explaining the body mass (g) of Wood Warbler nestlings (response variable). Shown are averaged coefficients and confidence intervals (CI) across models with $\Delta\text{AICc} < 2$ (Table 5; conditional average). Significant relationships ($P < 0.05$) are marked in bold. For the description of covariates see Table 3.

and hatched was comparable between nests with blowflies (mean 0.15, 95% CIs: 0.04–0.30, $n = 27$ nests) and those without (mean 0.22, 95% CIs: 0.06–0.43, $n = 59$).

Discussion

The results showed an inconsistent relationship between weather conditions during the two stages of Wood Warbler nestling development and blowfly infestation within the dome-shaped nests of the birds. In the early nestling stage, when chicks were young and adult female blowflies usually lay their eggs in bird nests^{14,25,27}, the likelihood of blowfly infestation increased if high ambient temperatures and low precipitation prevailed. Almost all of the nests infested with blowflies were exposed to ambient temperatures exceeding 15 °C, with little rain in the early nestling stage (Fig. 1a,b). A similar relationship was weak when weather conditions in the late nestling stage were tested. The intensity of blowfly infestation was unrelated to weather in the early nestling stage. However, in the late nestling stage, the number of blowflies was greater in infested nests that had been exposed to higher ambient temperatures during this period, but only if ants were absent from the same nests.

Moreover, the relationship between blowfly infestation and relative hatching date of Wood Warblers, or study year, appeared important only when the mean ambient temperature was dropped from the top hurdle models (on count or binomial parts). Thus, the increasing occurrence and intensity of blowfly infestation over a spring–summer breeding season, and the lowest occurrence of ectoparasites in 2020, seemed to also be related to ambient temperatures, which varied in the same manner within and between years (Supplementary Fig. S1, Supplementary Table S1). In contrast to some previous studies^{22,24,29,33}, blowfly infestation changed little in relation to Wood Warbler brood size or habitat type (deciduous vs mixed deciduous-coniferous stands). Furthermore, despite some variation in nest infestation of ectoparasites, Wood Warbler nestling growth was unrelated to blowfly abundance, although it tended to be generally lower at high rainfall.

Our observations supported the hypothesis that warm and dry weather promotes ectoparasite infestation of bird nests. The results were consistent with the study by Merino and Potti²², who recorded the lowest blowfly parasitism of Pied Flycatcher *Ficedula hypoleuca* nests during the coldest and wettest breeding season. Eeva and Klemola⁴⁶ also reported lower prevalence of *Protocalliphora* spp. in Pied Flycatcher nests if weather was cooler in the nestling period. A positive relationship between the intensity of blowfly infestation and ambient temperature was found in Blue Tit *Cyanistes caeruleus* nests in Corsica²³ and in Spain²⁴. Other studies showed inconsistent or insignificant relationships between weather during the nestling stage and blowfly nest infestation^{33,47}, but much wider time-windows were used, so probably a poorer match with the timing of greatest sensitivity of blowflies.

The more frequent blowfly infestation of Wood Warbler nests that had been exposed to warm and dry weather in the early nestling stage could be related to increased activity of adult female blowflies at ambient temperatures exceeding 15 °C, probably when seeking dry nests in which to oviposit^{26,27,30}. Warm weather might also influence the behaviour of a parent bird to shorten the brooding sessions and extend the time spent outside the nest⁴⁸. The changes in brooding activity of the birds may create more opportunities for adult blowfly females to oviposit on small, unfeathered nestlings, left alone by the parent. However, the elevated intensity of blowfly infestation in nests that had been exposed to warm weather in the late nestling stage, when larvae develop in bird nests, might be due to increased survival of larvae in warmer nests²⁹. Higher precipitation seemed to have no apparent impact on ectoparasite numbers, as the intensity of blowfly infestation remained stable in Wood Warbler nests regardless of rainfall levels, similar to an experimental study with dry and wetted nests³⁰.

Although nests are composed of insulating materials and are warmed from within by the host birds, the nest temperature strongly depends on ambient temperature^{21,49,50}. Thus, ambient conditions still could have a direct impact on developing blowfly larvae within unenclosed dome-shaped nests, with broadly similar insulative

protection as unenclosed, open-cup nests^{15–17}. As such, weather is likely to be an important proximate factor driving the prevalence and intensity of ectoparasite infestation in a range of bird nests.

As blowfly numbers were lower in nests containing ants, compared to nests without ants, the presence of the predatory insects might improve nest sanitation, particularly in warm weather when foraging ant workers could be more active^{37,38}. Although ant predation on blowflies has not been directly observed in this study, predatory ants removing other ectoparasites from bird nests has been previously documented³⁶. As such, a similar situation might have occurred in our study system, as predatory ant species were present in the warbler nests. Alternatively, the lower number of ectoparasites in nests with ants might result from reasons other than ant predation, such as chemical defence by ants towards different invertebrate species⁵¹. However, the developing blowfly larvae, as obligatory blood-sucking ectoparasites of birds, would be unlikely to escape from bird nests in this situation.

While more studies are needed to confirm the importance of ants in the sanitation of bird nests from ectoparasites, such intricate and weather-dependent mutualistic interactions might well occur between nesting birds and ants^{21,52,53}. A previous experimental study indicated that the body heat of birds can attract ants to colonise bird nests to raise their own broods (larvae or pupae) within the nest structure²¹. Ant colonisation of bird nests could be driven by the benefits of raising broods under more suitable thermal conditions than in the ants' own nests, particularly in cool and rainy weather⁵³. Thus, active nests of endothermic birds could be an important source of warm nesting-sites that are sought by ants in cool regions^{21,38}. Nevertheless, the current study suggests that the greatest potential benefits for birds hosting ants in their nests might occur in warm weather, when foraging ant workers may be active and potentially reduce the number of blowfly ectoparasites most effectively^{36,37}. If correct, weather might have contradictory impacts on the interspecific interactions between the nest owners (birds) and commensal ants, with shifting benefits for both taxa under varying ambient conditions. Further work would be worthwhile to confirm the plausible weather-dependent symbiotic interactions between nesting birds and ants, which might be another example of ecological links that are potentially sensitive to climate change³⁸.

Although cool weather and ant presence was associated with lower numbers of blowflies within infested warbler nests, contrary to our expectations there was no obvious relationship between the degree of blowfly infestation or ant presence and the growth or mortality of Wood Warbler nestlings. An insignificant impact of ectoparasites on songbird nestlings has also been reported in previous studies^{24,25,46,54}, suggesting that impacts were undetected or that birds were able to compensate for the costs of parasitism^{40,45,55,56}.

As blowfly larvae may aggregate and suck more blood from some of the nestlings in a brood, the detrimental impact of ectoparasites may be unevenly distributed among nestlings. This may consequently impede the detection of the relationship between blowfly abundance and the rate of nestling growth⁵⁷. Alternatively, parent birds may be able to offset ectoparasite infestation, perhaps by frequent feeding rates when food is abundant, such as in the old-growth stands of the Białowieża Forest⁵⁸. Nonetheless, blowfly infestation could have other negative effects on birds that we did not measure in this study. These effects could include anaemia^{59,60}, increased begging intensity of nestlings that elevates predation risk⁵⁵, or reduced survival or productivity of adults^{33,61}. As such, blowfly parasitism may still be costly for host birds^{14,25,31,55,60}.

The observed patterns of nestling growth in relation to rainfall could be due to direct effects of weather on birds by, for example, increasing heat loss and energy expenditure of nestlings in wet nests³⁹, particularly in smaller broods⁶², or by interrupting food provisioning by parents⁶³. However, high precipitation may also indirectly influence birds by reducing food availability, such as defoliating caterpillars or flying insects that constitute a large part of the diet of Wood Warbler nestlings^{41–43,64,65}. As such, weather could affect the growth of nestlings in multiple ways. Although there is ample evidence of proximate weather impacts on the breeding success and survival of breeding birds¹, understanding the influence of indirect impacts of ambient temperature or rainfall can be challenging, and requires further experimental approaches.

Conclusions

In summary, our study provides novel information on the potential intricate impacts of weather on species that cohabit within the microenvironments of bird nests. Similar to other ecological networks^{3,7,8}, ambient temperatures or rainfall appeared to directly influence the nest-dwelling arthropods and, to a lesser degree, the nesting birds. Additionally, weather conditions may also have cascading effects on host birds via interspecific interactions with ectoparasites and ants. However, further work is needed to confirm the role of ants in sanitising bird nests from ectoparasites at a range of ambient temperatures.

We found that the frequency of nest parasitism by blowflies was related to warm and dry weather in the early nestling stage, and blowflies were also more abundant in infested bird nests if higher ambient temperatures had occurred in the period of their larval development. As warm weather might improve nest sanitation by ants, the same ambient conditions may have conflicting impacts on ectoparasite abundance. However, neither the reduced nest infestation with blowflies, nor the presence of ants within bird nests, had a visible influence on warbler nestling growth or survival. The effect of weather on nestling growth was also rather weak, with only the length of primary feathers tending to be lower after high precipitation. Thus, birds seemed well able to tolerate unsuitable weather conditions and ectoparasite infestation in the old-growth stands of the Białowieża Forest, where superabundant food may help parents to compensate for the costs.

The study provides valuable information from a primeval temperate forest, little affected by direct human activity, which allows for future comparisons with investigations from human-altered habitats. The findings highlight the consequences of changing weather conditions for animals living within ecological networks, and may be particularly important in the era of climate change.

Material and methods

Study area. We conducted the study in the best-preserved stands of the Białowieża Forest, strictly protected within the Białowieża National Park (hereafter BNP; coordinates of Białowieża village: 52°42'N, 23°52'E). The extensive Białowieża Forest (c. 1500 km²) straddles the Polish-Belarusian border, where the climate is sub-continental with annual mean temperatures during May–July of 13–18 °C, and mean annual precipitation of 426–940 mm^{66,67}.

The forest provides a unique opportunity to observe animals under conditions that likely prevailed across European lowlands before widespread deforestation and forest exploitation by humans^{66,68,69}. The stands have retained a primeval character distinguished by a multi-layered structure, frequent fallen and standing dead trees, and a high species richness^{66,70}. The stands are composed of about a dozen tree species of various ages, up to several hundred years old. The interspecific interactions and natural processes have been little affected by direct human activity.

We conducted observations mostly within the three permanent study plots (MS, N, W), totalling c. 130 ha, and in other nearby fragments of primeval oak-lime-hornbeam *Tilio-Carpinetum* or mixed deciduous-coniferous *Pino-Quercetum* stands. However, a small number of observations from adjacent managed deciduous forest stands were also included. For details of the study area see^{71–73}.

Study species. Our study system focused on ground-nesting Wood Warblers *Phylloscopus sibilatrix*, blowflies *Protocalliphora azurea*, and *Myrmica* or *Lasius* ants, which occurred in the birds' nests.

The Wood Warbler is a small (c. 10 g) insectivorous songbird that winters in equatorial Africa and breeds in temperate European forests, typically rearing one or two broods each year⁷⁴. Wood Warblers build dome-shaped nests for each breeding attempt, composed of woven grass, leaves and moss, and lined with animal hair⁷³. The nests are situated on the ground among moderately sparse vegetation, often under a tussock of vegetation or near a fallen tree-branch or log (see examples in Supplementary Fig. S2)^{53,75}. The breeding season of Wood Warblers begins in late April–early May and ends in July–August, when nestlings from replacement clutches (after initial loss) or second broods leave the nest. The typical clutch size in BNP is 5–7 eggs, and the nestling stage lasts 12–13 days^{74,76}.

Wood Warbler nests are inhabited by various arthropods, including *Myrmica ruginodis* or *M. rubra* ants, and less often *Lasius platythorax*, *L. niger* or *L. brunneus*. The ants foraged and/or raised their own broods within the Wood Warbler nests⁵². The *Myrmica* and *Lasius* ant species are common in Europe^{77,78}. Their colonies contain from tens to thousands of workers, and can be found on the forest floor, e.g. in soil, within or under fallen dead wood, in patches of moss, or among fallen tree-leaves^{53,77,78}. All of the ant species found in the Wood Warbler nests are predators of other arthropods^{77,79,80}.

Blowflies, *Protocalliphora* spp., are obligatory blood-sucking (hematophagous) ectoparasites that reproduce within bird nests. The occurrence, abundance, and impact of blowflies on Wood Warbler offspring is largely unknown, similar to many other European songbirds that build dome-shaped nests. Adult blowflies emerge in late spring and summer to lay eggs on the birds' nesting material or directly onto the skin of typically newly hatched nestlings^{14,26}. The blowfly larvae hatch within two–three days, and develop in the structure of warm bird nests for another 6–15 days, during which they emerge intermittently to feed on host blood, before finally pupating within the nests^{14,25–27}.

Data collection. *Nest monitoring and measurements of nestlings.* We searched for Wood Warbler nests daily from late April until mid-July in 2018–2020, by following birds mainly during nest-building. Nests were assigned to a deciduous or mixed deciduous-coniferous habitat type, depending on the tree stand where they were found. We inspected nests systematically, according to the protocol described in Wesolowski and Maziarz⁷⁶. The number of observer visits was kept to a minimum to reduce disruptions for birds or potential risks of nest predation.

We aimed to establish the dates of hatching (day 0 ± 1 day), nestlings vacating the nest (fledging; ± 1 day) or nest failure (± 1–2 days). When nestlings hatched asynchronously, the hatching date corresponded to the earliest record of nestling hatching. The dates of fledging or nest failure were the mid-dates between the last visit when the nestlings were present in the nest, and the following visit, when the nest was found empty. Nest failure was primarily due to predation, which is the main cause of the Wood Warbler nest losses in BNP^{76,81} and elsewhere in Europe^{82,83}.

To assess fitness consequences for birds of variable weather conditions, blowfly abundance and/or ant presence, we measured nestling growth and determined brood reduction (i.e. the mortality of chicks in the nest) from hatching until fledging. To define brood reduction, we assessed the number of hatchlings (nestlings up to 4 days old) and the number of fledglings leaving the nests. To ensure accurate counting and avoid premature fledging of nestlings, we established the number of fledglings on the day of measurement, when all nestlings were temporarily extracted from the nest.

We measured nestling growth on a single occasion when they were 6–9 days old (median 8 days), almost fully developed but too young to leave the nest. The measurements lasted for less than 10–15 min at each nest to minimise any potential risk of attracting predators. For each nestling we measured (using a ruler) the emerged length of the longest (3rd) primary feather vane (± 0.5 mm) on the left wing^{84,85}, and body mass to the nearest 0.1 g using an electronic balance. The length of the feather vane is closely linked to feather growth⁸⁶ and is one of the characteristics of nestling growth^{85,87}. We treated the length of the primary feather vane and body mass as indices of nestling growth rate under varying conditions of weather, blood-sucking ectoparasites, or ant presence.

Extraction of arthropods from bird nests. To assess the number of blowflies and to establish the presence of ants, we checked the contents of 129 nests (including 11 nests from the managed forest stands) at which Wood Warbler nestlings had been measured. The sample included 86 successful breeding attempts (where a minimum of one nestling successfully left the nest), 27 failed (predated) nests (remnants of nestlings were found, but the nest structure remained intact), and 16 nests with an unknown fate (nestlings were large, so were capable of leaving the nest, but no family were located or other signs indicating fledging).

Due to ethical reasons, we were unable to collect the Wood Warbler nests and extract the ectoparasites and ants from them while they were in use by the birds. Removing the nests and replacing them with dummy nests would cause unacceptable nest desertion by adults. Therefore, we assessed the occurrence and number of blowflies or ant presence after Wood Warbler nestlings fledged or the breeding attempts failed naturally. We retrospectively explored the changes in blowfly infestation¹⁴, including the effect of ant presence⁵³ in the same nests.

We collected nests from the field as soon as a breeding attempt ended, within approximately five days (median 1 day) following fledging or nest failure (nest structure remained intact). The delay of nest collection would not bias the ectoparasite infestation, as blowfly larvae pupate within bird nests and stay there after the hosts abandon their nests; puparia can be still found in nests collected in autumn or winter¹⁴. As the likelihood of finding ant broods (larvae or pupae associated with workers) was rather stable with the delay of nest collection⁵³, the method seemed reliable also for assessing the presence of ant broods (35 of all 71 Wood Warbler nests containing ants). Only the number of nests with lone foraging ant workers could be underestimated, potentially inflating the uncertainty of tested relationships. However, as ants usually re-use rich food resources⁸⁸, foraging *Myrmica* or *Lasius* ant workers might regularly exploit warbler nests, increasing the chances of finding the insects in the collected nests.

Wood Warbler nests were collected in one piece, with each placed into a separate sealed and labelled plastic bag. We carefully inspected the leaf litter around the nests, and the soil surface under them, to make sure that all blowfly larvae or pupae were collected. We transported the collected nests to a laboratory, where we stored them in a fridge for up to 5–6 days before the arthropod extraction.

To establish the number of blowflies and the presence of ants, in 2018, we carefully pulled apart the nesting material and searched for the arthropods amongst it⁵². We gathered all blowfly pupae or larvae and a sample of ant specimens into separate tubes, labelled and filled with 70–80% alcohol, for later species identification. For nests collected in 2019–2020, we extracted the arthropods with a Berlese-Tullgren funnel. During the extraction, which usually lasted for 72 h, each nest was covered with fine metal mesh and placed *c.* 15 cm under the heat of a 40 W electric lamp. The arthropods were caught in 100 ml plastic bottles containing 30 ml of 70–80% ethanol, installed under each funnel. After the arthropod extraction, we carefully inspected the nesting material in the same way as in 2018, to collect any blowflies that remained within the nests. The quality of information collected on the number of ectoparasites and ant presence should be comparable each year.

Weather data. We obtained the mean daily temperatures and rainfall sums from a meteorological station, operated by the Meteorology and Water Management National Research Institute in the Białowieża village, 1–7 km from the study areas.

Data analyses. *Weather conditions affecting blowfly ectoparasites.* To explore the impact of weather on blowfly ectoparasites, for each Wood Warbler nest we calculated average temperatures from daily means, and total sums of rainfall from daily sums, for the two time-windows in which we assumed the impact of weather would be of greatest importance:

- i. the early nestling stage, when Wood Warbler nestlings were 1–4 days old. During this stage, female blowflies require a minimum temperature of *c.* 16 °C to become active and oviposit in bird nests²⁷. Thus, cool and wet weather in the early nestling stage should reduce the activity of ovipositing blowflies, leading to less frequent ectoparasite infestation of Wood Warbler nests.
- ii. The late nestling stage, when the warbler nestlings were aged between over four days old and until fledging or nest failure. During this stage, blowfly larvae grow and develop in bird nests after hatching a few days after oviposition^{14,25–27}. As the temperature of bird nests strongly depends on ambient temperatures²¹, mortality of blowfly larvae should increase in cool weather, resulting in fewer ectoparasites in nests collected shortly after the fledging of birds²⁹.

Weather conditions affecting Wood Warbler nestling growth. To explore the impact of weather on nestling growth, for each nest we calculated the average temperatures and total sums of rainfall for the period when nestlings were over four days old and until their measurement, usually on day 8 from hatching (see above). During this stage, nestlings are no longer brooded by a parent⁷⁴, so must balance their energetic expenditure between growth (feather length and body mass) or thermoregulation⁸⁹. Thus, we expected that the gain in body mass and the growth of flight feathers would be reduced in nestlings during cool and wet weather, when maintaining a stable body temperature would be costly⁹⁰.

Statistical analyses. All statistical tests were two-tailed and performed in R version 4.1.0⁹¹.

The changes in blowfly infestation of the Wood Warbler nests. To test the changes in blowfly infestation of warbler nests, we used zero-augmented negative binomial models (package *pscl* in R;^{92,93}), which deal with the problem of overdispersion and excess of zeros⁹². In this study, hurdle and zero-inflated models fitted with the

same covariates had an almost identical Akaike Information Criterion (AIC). Therefore, we presented only the results of hurdle models, which are easier to interpret than zero-inflated models. Hurdle models consisted of two parts: a left-truncated count with a negative binomial distribution representing the number of blowflies in infested nests, and a zero hurdle binomial estimating the probability of blowfly presence. We used models with a negative binomial distribution, which had a much lower AIC than with a Poisson distribution on a count part.

We designed the most complex (global) model that contained a response variable of the number of blowflies in each of the 129 Wood Warbler nests. The covariates were: mean ambient temperature, total sum of rainfall, presence (or absence) of ants in the same nests, habitat type (deciduous vs mixed deciduous-coniferous forest), study year (2018–2020), the number of nestlings hatched (brood size), and nest phenology (the relative hatching date of Wood Warbler nestlings, as days from the median hatching date in a season: 23 May in 2018, 25 May in 2019 and 29 May in 2020). The initial global model also contained the two-way interaction terms that we suspected to be important: between temperature and rainfall, temperature and presence of ants, and rainfall and presence of ants.

To explore all potentially meaningful subsets of models, we used the same covariates on both parts (count and binomial) of the global model. We performed automated model selection with the MuMIn package⁹⁴, starting from the most complex (global) model and using all possible simpler models (i.e. all subsets)⁹⁵. To attain the minimum sample size of *c.* 20 data points for each parameter⁹⁶, we limited the maximum number of parameters to six in each part (count or binomial) of the candidate models.

As some of the interaction terms appeared insignificant in the initial model selection, to minimise the risk of over-parametrisation, we included only the significant interaction term on a count part of the final global model. As described above, we performed model selection again. We tested linear relationships, as the quadratic effects of weather variables (presuming temperature or rainfall optima) appeared insignificant.

To test whether blowfly infestation changed with weather in the early or late nestling stages, we twice repeated the procedure described above. The first global model included the mean ambient temperature and the total sum of rainfall for the early nestling stage, and the second global model contained weather variables for the late nestling stage. The remaining covariates were the same.

A practice of including the same sets of covariates on count and binomial parts has been previously questioned⁹⁷. However, our approach allowed us to comply with these objections⁹⁷, as we presented only the most parsimonious models (with $\Delta\text{AICc} < 2$) which all contained different sets of covariates on count and binomial parts.

We considered models differing by less than two AICc units from the best fitting model (with smallest AICc) as equally informative⁹⁸. We averaged the top models, always with different sets of covariates on count and binomial parts, by using conditional averaging, to obtain parameter estimates and their 95% CIs reflecting model selection uncertainty.

The analyses comprised successful ($n = 86$) and other nests that failed in the late nestling stage (nest structure remained intact; $n = 27$) or their fate was unknown (nestlings were large enough to escape a predator attack; $n = 16$). Including failed nests or those with the unknown status increased sample sizes, and was justified because the same patterns emerged when only the successful breeding attempts were analysed.

We calculated bootstrapped means and 95% CIs (10,000 random re-samplings), to present the number of blowflies in infested nests with and without ants, or in different years.

The growth of Wood Warbler nestlings. To explore the changes in the growth of Wood Warbler nestlings with varying weather conditions, blowfly abundance, ant presence, or other factors (relative hatching date, brood size, nestling age, habitat type, study year), we used linear mixed effect models, with package glmmTMB⁹⁹. In the analysis we employed the data from 2018 to 2020 for the length of the third primary feather and body mass of 742 nestlings from 129 Wood Warbler nests. The models contained a random intercept for nest identity that accounted for non-independent growth rates of nestlings from the same nests.

We modelled the length of the third primary feather or body mass, both assessed *c.* 8 days post-hatching, as responses to nine predictors: mean ambient temperature and total sum of rainfall in the stage when nestlings were over four days old and until their measurement, blowfly abundance (i.e., the number of blowflies per nestling in nests with and without blowflies), presence or absence of ant workers, and also habitat type (deciduous vs mixed deciduous-coniferous), study year, relative hatching date of birds, brood size, and nestling age (number of days since hatching on day 0). In models, we included nestling age to correct for deviations from the intended measurement age at 8 days post-hatching.

For both measures of nestling growth (feather growth and body mass), global models initially contained main effects of all covariates mentioned above and the potentially important two-way interaction terms between temperature and rainfall, temperature and blowfly abundance, rainfall and blowfly abundance, and temperature and ant presence. However, as none of the interaction terms appeared significant, we tested only the main effects. All models included only linear relationships, as none of the quadratic effects (presuming temperature or rainfall optima) were significant.

To create a subset of models with variables best explaining the growth of Wood Warbler nestlings, we used an automated model selection in MuMIn⁹⁴, according to an information-theoretic approach. This method allowed us to find the most parsimonious models among the candidate model set, which were drawn from the most complex (global) model⁹⁸. To attain the minimum sample size of *c.* 20 data points for each estimated parameter⁹⁶, we limited the maximum number of parameters to six in the candidate models. We considered models differing by less than two AICc units from the best fitting model (with smallest AICc) as equally informative⁹⁸. We averaged these top models (using conditional averaging) to obtain parameter estimates and their 95% CIs reflecting model selection uncertainty.

Mortality of Wood Warbler nestlings. To test whether the nest infestation with blowflies increased the mortality of Wood Warbler nestlings, we compared brood reduction (i.e. the difference between the number of fledglings and hatchlings) in 86 successful nests with and without ectoparasites, based on bootstrapped means and 95% CIs (10,000 random resamplings).

Data availability

The datasets analysed during the current study are available in the Figshare repository, <https://doi.org/10.6084/m9.figshare.21229472.v1>¹⁰⁰.

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Author contributions

M.M. designed the study, collected data, performed analyses and prepared the draft of the paper; R.K.B. designed the study, collected data and contributed to the writing; P.C. performed analyses and contributed to the writing; G.H. designed the study, collected data, and contributed to the writing.

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Competing interests

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Additional information

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