

1 **Parasite prevalence increases with temperature in an avian**
2 **metapopulation in northern Norway**

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21 Abstract

22 Climate and weather conditions may have substantial effects on the ecology of both parasites and
23 hosts in natural populations. The strength and shape of the effects of weather on parasites and
24 hosts are likely to change as global warming affects local climate. These changes may in turn
25 alter fundamental elements of the parasite-host dynamic. We explored the influence of
26 temperature and precipitation on parasite prevalence in a metapopulation of avian hosts in
27 northern Norway. We also investigated if annual change in parasite prevalence was related to
28 winter climate, as described by the North Atlantic Oscillation. We found that parasite prevalence
29 increased with temperature within-years and decreased slightly with increasing precipitation. We
30 also found that a mild winter (positive winter NAO index) was associated with higher mean
31 parasite prevalence the following year. Our results indicate that both local and large scale
32 weather conditions may affect the proportion of hosts that become infected by parasites in
33 natural populations. Understanding the effect of climate and weather on parasite-host
34 relationships in natural populations is vital in order to predict the full consequence of global
35 warming.

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37 **Key words:** Climate, house sparrow, NAO, parasite, precipitation, prevalence, Syngamus
38 trachea, temperature

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44 Key findings

- 45 - Parasite prevalence increases with temperature
- 46 - Parasite prevalence increases following a mild winter
- 47 - Precipitation had little effect on parasite prevalence
- 48 - Climate and weather may influence parasite prevalence

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50 Introduction

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52 The relationship between parasites and climate has received increasing attention in recent years
53 due to global climate change (see Harvell *et al.* 2002; Altizer *et al.* 2013). Parasites may have a
54 significant negative effect on growth rates of host populations through their effect on fitness of
55 individual hosts (Anderson and May 1978; May and Anderson 1978). Climate change may alter
56 important aspects in the parasite-host relationship (e.g. transmission rate) and potentially lead to
57 drastic changes in the population dynamics of both parasites and hosts (Harvell *et al.* 2002;
58 Altizer *et al.* 2013). One important parameter that may be altered is the percentage of hosts
59 infected in a population at a given time, i.e. parasite prevalence. Several experimental and
60 observational studies have indicated that variation in climatic parameters may affect the parasite
61 prevalence in a population (see Harvell *et al.* 2009; Lafferty 2009), both direct and indirectly.
62 For example, Zamora-Vilchis *et al.* (2012) found that prevalence of blood parasites was higher in
63 bird populations that inhabited areas with higher annual temperatures. They attributed this
64 pattern to both higher vector abundance and faster development of the parasites at higher
65 temperatures. Along with temperature, there has also been a call for more studies which also
66 investigate the effects of precipitation (Altizer *et al.* 2013). Precipitation may have a direct

67 influence on parasite prevalence, for example through desiccation of free-living parasite eggs or
68 larvae (e.g. Hudson and Dobson 1991; Miterpakova *et al.* 2006; Jex *et al.* 2007) or indirectly
69 through other mechanisms such as vector availability (Sacks *et al.* 2004). Furthermore, host
70 demography may play an important role in the parasite-host relationship (see Dobson 1990). For
71 instance, transmission of parasites may increase with host population density (Anderson and
72 May 1978), which in turn may increase prevalence (Arneberg 2001). Parasites often have an
73 aggregated distribution with respect to host individuals (see Wilson *et al.* 2002). Therefore,
74 reliable estimates of parasite prevalence require sampling of a large proportion of the host
75 population (Wilson *et al.* 2002). In addition, because parasite prevalence may differ between
76 different classes of individuals (e.g. adults vs. juveniles), sampling should be stratified (i.e. equal
77 proportion of different groups) in order to avoid bias in estimates of prevalence.

78 In the present study we explore the relationship between climate and prevalence of the
79 parasitic nematode *Syngamus trachea* in a metapopulation of house sparrows (*Passer*
80 *domesticus*) in northern Norway over a 7-year period. Our aim was to investigate whether
81 within-year variation in prevalence of *Syngamus trachea* could be explained by temperature,
82 precipitation and population density. We also investigated the relationship between prevalence
83 among years and the preceding winter climate estimated by the North Atlantic Oscillation index
84 (NAO).

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86 Material and methods

87 Study area

88 The study was carried out in an archipelago consisting of 18 islands in the Helgeland district in
89 northern Norway (Supplementary Fig. S1). The house sparrows on these islands have been

90 studied on an individual based level by capture-mark-recapture methods since 1993 (Holand *et*
91 *al.* 2016). In this study we focus on 4 of the islands (Aldra, Gjerøy, Hestmannøy and Indre
92 Kvarøy), where the sparrows mainly live in colonies on dairy farms. House sparrows shelter
93 inside farm buildings when the weather is harsh, especially in winter. A high proportion of
94 individuals have been individually marked (> 90%), the annual recapture probability is high (>
95 70 %), and fecal samples have been collected since 2007. Individuals have often been captured
96 and sampled several times during their lifetime. Because of the sedentary nature of the house
97 sparrows, the large size of the study area and the high proportion of individually marked
98 individuals in our metapopulation, we can identify individuals that move between islands in the
99 study area (Pärn *et al.* 2012).

100

101 Study species

102 The parasite of interest in this study is the nematode worm *Syngamus trachea* (henceforth *S.*
103 *trachea*). *S. trachea* has a cosmopolitan distribution and has been found in most terrestrial bird
104 genera (Atkinson *et al.* 2008). In Norway the parasite has been recorded in several wild bird
105 species (for list see Bakke 1973). The parasite is known as “gapeworm” in the poultry industry,
106 where outbreaks have caused substantial problems (Atkinson *et al.* 2008). *S. trachea* has a
107 lifecycle that may include a paratenic host (earthworms, snails or insects) in addition to the final
108 avian host. The parasite(s) feed on blood in the trachea tissue causing mechanical damage,
109 anaemia, inflammation and excess mucus production. The birds that are infected may develop
110 symptoms consisting of gasping, wheezing and shaking of the head. This discomfort may affect
111 food uptake, which combined with blood loss and the symptoms listed above, can cause death
112 (Atkinson *et al.* 2008). The prepatent period (i.e. the time between infection and first egg

113 produced by the parasite) is 12-17 days in chickens (*Gallus gallus*) and the adults can live 2-4
114 months (Barus 1966b). Males and females join in permanent copulation and the female releases
115 eggs which are passed in the feces of the host (Atkinson *et al.* 2008). The development time of
116 embryos into third stage invasive larvae depend on temperature, and has a lower limit of 16 °C
117 (Barus 1966a). For temperatures over 16 °C the development time may vary from ca. 45 days at
118 17 °C to ca. 7 days at 29 °C (Barus 1966a). At temperatures above 29 °C the development time
119 increases, becomes irregular and stops at 35-37 °C (Barus 1966a). Barus (1966a) found that eggs
120 could be vulnerable to desiccation and may become incapable of further development after 14
121 days of exposure to the daily varying temperature (12-24 °C) and humidity (36-97 %). It was also
122 found that c. 35 % of eggs died when exposed to temperatures between -15 - -25 °C for 45 days.

123 The house sparrow is a small passerine bird with a global distribution, and is widely
124 distributed on the Northern hemisphere (Anderson 2006). The house sparrows live in close
125 association with human settlements. During winter their diet mainly consist of cattle food, and
126 seeds from cultivated crops (Anderson 2006). In the summer the house sparrows forage
127 outdoors, to a large extent, on different types of seeds and insects (Anderson 2006).

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129 Field work, climate data and population size

130 We captured house sparrows using mist-nets and placed the birds in paper bags with a small hole
131 at the top to prevent asphyxiation. After approximately 10 minutes in the paper bag, a fecal
132 sample had usually been obtained. Samples were stored in 1 ml of MilliQ H₂O in a 1.5 ml cryo-
133 tube at between 1 and 8 °C until analyzed. Samples were analyzed by flotation of eggs in a
134 McMaster egg counting chamber (see Holand *et al.* 2013 for detailed descriptions). During 2007
135 – 2013 (1st May – 8th November), 3619 fecal samples were collected from 1705 individuals.

136 Detection of eggs from *S. trachea* in bird feces is a reliable and consistent method of monitoring
137 prevalence in host populations (Barus 1966b; Barus 1966c). To our knowledge, *S. trachea* does
138 not present a circadian rhythm in the release of eggs. In addition to captures, we also visited
139 nests in the populations and marked fledglings when they were c. 11 days old.

140 Weather data was obtained from Norwegian Meteorological Institute's weather stations
141 on the islands Myken and Solv er in the Helgeland archipelago (Supplementary Fig. S1). High
142 spatial correlation in daily mean temperature ( C) and daily precipitation (mm) has been found
143 between the two weather stations (Ringsby *et al.* 2002). When choosing our weather predictor
144 variables, the life-history of the parasite was considered. The time between infection and first
145 egg produced by the parasite (prepatent period) is c. 15 days (see above). During this period we
146 assumed that weather had little or no impact on the parasite. Furthermore, we assumed that the
147 mean weather conditions during a 20-day time-window before the prepatent period was likely to
148 capture the important period during which the weather conditions (temperature and precipitation)
149 may influence the development time of infective larvae (see above). This would allow us to
150 investigate if variation in the mean weather conditions preceding our sample explained the
151 individual probability of infection by *S. trachea*. As an index of large-scale climatic variation we
152 used station based Hurrell North Atlantic Oscillation index (NAO) for winter months (December
153 – March). The data was obtained from the National Center for Atmospheric Research, USA. This
154 index is based on the difference in normalized atmospheric pressure at sea level between Lisbon,
155 Portugal and Reykjavik, Iceland. In Scandinavia, a positive winter NAO index is correlated with
156 milder and wetter winters whereas a negative NAO index is correlated with colder and dryer
157 winters (Hurrell 1995).

158 An estimate of population size on a given day of the year was obtained from estimates of
159 the number of alive adults and simulations of a model of daily juvenile mortality rates as a
160 function of fledging date of nestlings (for detailed method, see Supplementary information S1).
161 Relative daily population size within each sub-population was calculated by subtracting the mean
162 population size and dividing by the standard deviation (i.e. a z-score transformation). Assuming
163 that the size of the suitable habitat in the subpopulations did not change in the period, this
164 estimate corresponds to population density at a given day and subpopulation. We also calculated
165 the mean population density in a 20-day time-window before the prepatent period as we assumed
166 that this was likely to influence parasite prevalence (same as weather variables, see above)

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169 Statistical analyses

170 All analyses were done using the statistical software package R version 3.5.1 (R Core Team
171 2018). The focal response variable in the statistical analyses was individual infection status. We
172 defined an individual as infected (status = 1) if at least one egg of *S. trachea* were found in the
173 fecal sample. If no eggs were found, the infection status was set to 0. We modeled infection
174 status (prevalence) using generalized linear mixed models (package glmmTMB version 0.2.2.0)
175 with a Bernoulli response variable (i.e. whether an individual was infected or not) and a logit link
176 function. Because many individuals (N = 774) were sampled more than once within a season, we
177 included a random intercept for individual identity to avoid pseudoreplication. We have
178 previously shown (Holand *et al.* 2013) that prevalence varies within season, islands and among
179 demographic groups in the study area. We therefore included the main effect of: life-stage group
180 (LSG: juvenile, adult male or adult female), island and seasonal day number (SDN). SDN was

181 the date when a bird was sampled, where day 1 was 1st of January. In addition, Holand *et al.*
182 (2013) found substantial variation in prevalence among years. A random intercept for year was
183 therefore included in all models. To test if the effects of weather on prevalence varied during the
184 season, we included the two-way interactions between weather variables and SDN. We also
185 included second order terms of the weather variables and the population density variable in order
186 to evaluate nonlinear effects of these respective variables. No higher-order terms (interactions or
187 quadratic terms) were included without the presence of the respective main effects of the term.
188 The NAO index was included as a yearly variable (i.e. one estimate for each year in the study).
189 To increase interpretability of interaction terms, we centered SDN and the two weather variables
190 on zero (i.e. mean = 0). In order to prevent possible effect of multicollinearity, all explanatory
191 variables were assessed for collinearity visually, by the use of Pearson's correlation coefficient
192 (r_p) and variance inflation factors (VIF, see Dormann *et al.* 2013). Candidate models were ranked
193 using Akaike information criterion corrected for small sample sizes (AIC_C), which penalizes
194 models with a high number of parameters relative to sample size (Burnham and Anderson 2002).
195 Estimates from models are reported as mean \pm 1 standard error (SE).

196 We also tested the correlation between observed annual mean prevalence in July and the
197 winter NAO index ($n = 7$). July was the month with largest sampling size of feces in our study
198 system (Holand *et al.* 2013).

199

200 Results

201 Six models obtained a $\Delta AIC_C < 2$ in our model comparison (Table 1). Among these, the second
202 highest ranked model contained the fewest number of parameters and may be considered the
203 most parsimonious. The five alternative models contained some of the parameters that were

204 present in the second highest ranked model (Table 1). All of our highest ranked models
205 contained a quadratic effect of temperature on parasite prevalence (Fig. 1 A), which indicated
206 that parasite prevalence increased to a peak at 12.37 degrees Celsius and then leveled out at very
207 high temperatures (see Fig. 1 A and Table 1). All the highest ranked models also contained a
208 negative effect of precipitation on parasite prevalence, (see Fig. 1 B and Table 1). The five
209 alternative models also contained interactions between SDN and temperature and precipitation
210 respectively, but the uncertainty of parameter estimates was large and impeded any
211 interpretations. All of the six top models contained a positive effect of NAO on parasite
212 prevalence (Fig. 1 C and Table 1). Finally, there was a strong positive correlation between mean
213 parasite prevalence in July and NAO ($r_p = 0.83$, $n = 7$, $t = 3.38$, $P = 0.02$, Fig. 2).

214

215 Discussion

216 This study has found that climate and weather can be important factors in explaining variation in
217 parasite prevalence patterns in natural populations of hosts. Our study also indicated that large
218 scale climatic patterns measured as NAO, may have a substantial impact of parasite prevalence
219 in wild populations of hosts.

220 Specifically, we found that within-year prevalence of *S. trachea* was positively associated
221 with temperature (but less so at very high temperatures). This supports previous qualitative
222 studies conducted by Barus (1966), who observed that prevalence of *S. trachea* in domestic birds
223 increased during the year as the temperature increased. Similar increases in prevalence within
224 years have been found for other parasite species and hosts (e.g. Karvonen *et al.* 2010; Paredes-
225 Esquivel *et al.* 2012; Bottari *et al.* 2013). The underlying mechanisms for a positive relationship
226 between parasite prevalence and within-year temperature may be difficult to determine.

227 However, studies have shown that thresholds in temperature may make it very difficult for
228 certain parasites to complete their life cycles due to reduced larvae survival probability or
229 prolonged egg development time at certain temperatures (e.g. Barus 1966a; O'Connor *et al.*
230 2006; Tinsley *et al.* 2011). This may typically limit transmission of parasites to the summer
231 season in arctic regions (Kutz *et al.* 2005; Jenkins *et al.* 2006; Hoberg *et al.* 2008). Several studies
232 have also shown that development rates of parasite eggs and larvae increase with temperature
233 (Hoar *et al.* 2012; Leathwick 2013). This may increase transmission rate at higher temperatures
234 (Kutz *et al.* 2005) and may lead to higher parasite prevalence.

235 Our results suggested that high levels of precipitation reduced parasite prevalence.
236 However, we found only minor changes in predicted prevalence for each mm of increased
237 precipitation (Fig.1 B). Thus, although eggs and larvae of *S. trachea* may generally be
238 susceptible to desiccation (see Material and Methods), this does not seem to a limiting factor in
239 our study system. We found no effect of population density on prevalence of *S. trachea* in our
240 subpopulations. This was somewhat surprising given that studies often suggest that prevalence
241 should increase with increasing population density (see Introduction). However, there may be a
242 more complex relationship between population density and transmission rates in our populations.
243 For example, parasite prevalence and transmission rates could be affected by heterogeneity in
244 parasite resistance of individual hosts (Borg *et al.* 2011, Lundregan *et al.* unpublished results).
245 Alternatively, one or more of our assumptions used to estimate population density may have
246 caused a weakening of the relationship between parasite prevalence and the true population
247 density.

248 Interestingly, all the highest ranked models included the annual winter NAO index, where
249 mild winters were associated with higher prevalence the following sampling period (1 May – 8

250 November). This result was also shown as a very strong positive correlation between winter
251 NAO index and observed mean prevalence in July the following summer (Fig. 2). However,
252 these results were based on only 7 NAO values (7 years) and should therefore be interpreted with
253 some caution. Given that this relationship is valid, it may be generated via several mechanisms.
254 First, it is known that many free-living stages of parasites (including *S. trachea*) have a relatively
255 low tolerance to temperatures below 0 °C and may suffer an increased mortality due to low
256 temperatures during winter (Barus 1966a; O'Connor *et al.* 2006; Descamps 2013; Sherrard-Smith
257 *et al.* 2013). A mild winter may result in increased winter survival of eggs and larvae, which in
258 turn may increase the parasite prevalence in the host population the following summer.
259 Alternatively, mild winters may result in increased survival probability of host individuals with a
260 poor body condition that may be more susceptible to infection the following summer. Second, a
261 positive winter NAO index is often associated with milder spring temperatures (Helama and
262 Holopainen 2012) and could therefore result in a longer transmission window for the parasite.
263 Finally, a positive winter NAO index might lead to a higher abundance of paratenic hosts
264 (insects) the following summer (Westgarth-Smith *et al.* 2012), thereby facilitating the
265 transmission of *S. trachea* to its avian hosts. Some climate models have predicted that
266 frequencies of positive winter NAO index's may increase in the future (Kuzmina *et al.* 2005).
267 This could lead to significant changes in the parasite-host relationship in the future. For instance,
268 as global warming is predicted to result in wetter and milder winter temperatures in northern
269 Europe (Alcarro *et al.* 2007), the present study suggests that parasite species which are limited
270 by low temperatures during the winter season may extend their geographical distribution to
271 higher altitudes and latitudes as a consequence. Understanding how climate impacts parasites
272 and hosts may be vital in accurately predicting the changes in natural communities due to climate

273 change (Altizer *et al.* 2013). Such knowledge may prove crucial in conservation and
274 management efforts of threatened species and ecosystems (Harvell *et al.* 2002).

275

276 Acknowledgements

277 We would like to thank everyone involved in the house sparrow project for help with fieldwork
278 and Grethe Stavik Eggen, Randi Røsbak and Henriette Vaagland for help with analyzing fecal
279 samples. We are also grateful to everyone at Centre for Biodiversity Dynamics (CBD), NTNU,
280 for helpful comments and help with statistics in R.

281

282 Financial support

283 This study was funded by the Research Council of Norway (RCN grant no. 274930), the RCN's
284 Centres of Excellence funding scheme (grant no. 223257), and the Norwegian University of
285 Science and Technology. The research was carried out in accordance with permits from the
286 Norwegian Animal Research Authority, the Norwegian Environment Agency, and the Bird
287 Ringing Centre at Stavanger Museum, Norway.

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433 disease in a warming climate. *Plos One*, 7(6), e39208. doi: e39208
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435

436 **Tables**

437 Table 1: Parameter estimates (± 1 SE) of the six best models (according to AIC_C) of parasite prevalence (*Syngamus trachea*) in a
 438 metapopulation of house sparrows in Norway. Models were fitted using generalized linear mixed models. Estimates are shown for
 439 each variable contained in the model. In addition, all models also contained the main fixed effect of island, life stage group (adult
 440 male, adult female, juvenile) and random intercept effects of individual identity and year. T = temperature, P = precipitation, SDN =
 441 season day number, df = degrees of freedom. All estimates are given with ± 1 SE.

442

443

Model	Intercept	SDN	NAO	T	T ²	P	P ²	T : SDN	P : SDN	df	ΔAIC_C
1	-7.410 \pm 0.508	0.0004 \pm 0.0033	0.256 \pm 0.050	0.454 \pm 0.069	-0.085 \pm 0.019	-0.086 \pm 0.037			0.001 \pm 0.001	14	0
2	-7.429 \pm 0.508	0.0008 \pm 0.0032	0.269 \pm 0.049	0.477 \pm 0.067	-0.084 \pm 0.019	-0.047 \pm 0.024				13	0.08
3	-7.352 \pm 0.507	0.0003 \pm 0.0033	0.268 \pm 0.051	0.468 \pm 0.070	-0.084 \pm 0.019	-0.052 \pm 0.047	-0.004 \pm 0.004		0.001 \pm 0.001	15	0.73
4	-7.432 \pm 0.509	0.0004 \pm 0.0033	0.241 \pm 0.052	0.429 \pm 0.073	-0.069 \pm 0.025	-0.081 \pm 0.037		-0.002 \pm 0.002	0.001 \pm 0.001	15	1.04
5	-7.445 \pm 0.509	0.0007 \pm 0.0032	0.259 \pm 0.051	0.461 \pm 0.071	-0.073 \pm 0.025	-0.040 \pm 0.026		-0.001 \pm 0.002		14	1.56
6	-7.375 \pm 0.508	0.0003 \pm 0.0033	0.253 \pm 0.053	0.442 \pm 0.074	-0.067 \pm 0.025	-0.048 \pm 0.047	-0.004 \pm 0.004	-0.001 \pm 0.002	0.001 \pm 0.001	16	1.74

444

445 **Figure legends**

446

447 Fig.1 Predicted values (solid line) from the most parsimonious model (based on AICc) for
448 prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast
449 of Helgeland, Norway. (A) The effect of within-year variation in temperature, (B) precipitation,
450 and (C) winter NAO index. All predicted values are shown with 95 % confidence intervals
451 (grey).

452 Fig. 2: The relationship between winter NAO index and observed mean prevalence of the
453 parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast of Helgeland,
454 Norway, in the month of July. Estimates of mean July prevalence are shown with ± 1 standard
455 error.

456



