Title: Lower survival probability of house sparrows severely infected by the gapeworm parasite.

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Abstract

The effect of parasites in natural populations has received increasing attention in recent years. Studies have shown that parasites may play an important part in population ecology due to their potential effects on host fitness. The main purpose of the present study was to investigate the effect of a nematode parasite (gapeworm, *Syngamus trachea*) on survival probability of house sparrows (*Passer domesticus*) from six natural populations located on 4 islands in the Helgeland archipelago in northern Norway. Infection status was obtained from feces samples collected from 603 house sparrows in the summer and autumn of 2007 - 2011. We also collected data on a visible symptom of severe infection (gasping for air) in 1391 house sparrows in the summer and autumn 2004-2011. We took advantage of recent advances in disease modeling in a multievent capture-mark-recapture framework to account for imperfect observations (state uncertainty). Each dataset was separately analyzed, in both analyses the relationships of year, island, individual body condition, age class and population density with survival probabilities. The relationship between infection (determined by feces egg counts) on annual survival of house sparrows was not statistically significant. However, the probability of annual survival was found to be significantly lower for adult house sparrows exhibiting a symptom of severe gapeworm infection, gasping for air. The present study demonstrates that severe infection by a parasite can have a negative relationship with survival probability of short lived avian hosts in wild populations.

Key words: Fitness, gapeworm, house sparrow, metapopulation, Survival , *Syngamus trachea*.

Introduction

The presence of parasites in natural populations may result in reductions of average fitness of host individuals, measured as survival probability or lifetime reproductive success (Gulland 1992, Hudson et al. 1992, Møller et al. 2009). Historically, the effects of parasites on host population dynamics were assumed to be of minor importance (Lack 1954). This view was changed by the milestone work of Anderson and May (1978) where they established a theoretical framework that described how parasites can have a regulatory/destabilizing effect on the population dynamics of hosts. This was first observed in red-grouse (*Lagopus lagopus scoticus*) populations (Hudson et al. 1998 but see also Albon et al. 2002, Pedersen and Greives 2008). The importance of parasites in host population dynamics may potentially be severely underestimated by observational studies (Tompkins et al. 2002). Anderson (1995) provides an example of how this may happen if the proportion of hosts that suffer mortality as a consequence of infection is directly proportional to the growth rate of the population. If an observational study is conducted when the host population has a low growth rate, the mortality caused by the parasite and the prevalence of the parasite may be very low (Anderson 1995). This may lead the observer to wrongly conclude that the parasite has little or no effect on the host population when the parasite is in fact regulating the population (Anderson 1995).

A parasite may cause the death of the host, and itself, while increasing its fitness (Hudson and Dobson 1991). The effects of parasites may differ among host individuals in a population. For example, compared to adults, juveniles which are going through major ontogenetic changes may be particularly vulnerable and suffer more from a parasite infection (Loman 1980, Souchay et al. 2013). Ultimately, the total impact of parasites on host fitness may depend on complex interactions between the virulence (i.e. the tendency to lead to host mortality) of the parasite and factors affecting host vulnerability to infection and individual fitness. Virulence of parasites is expected to be relatively high when the natural mortality rate of hosts is high (Poulin 2007). This relationship is caused by the expected positive relationship between parasite reproduction rate and virulence (Poulin 2007).

When studying the effect of parasites on host fitness, such as annual survival, one challenge will be to disentangle the relative importance of the parasite versus other factors. Variation in phenotypic traits has been shown to strongly influence survival of many species, and in particular individual variation in body mass and body condition (e.g. Ringsby et al. 1999, Naef-Daenzer et al. 2001, Blums et al. 2005). Body condition has been shown to be related to parasite load (e.g. de Lope et al. 1998, Neuhaus 2003, Tomas et al. 2008). Demographic properties, such as population density may also affect host fitness (Begon et al. 2005). Substantial negative density-dependent effects on survival have been detected as population size increases (Arcese et al. 1992, Norman and Peach 2013). High population density is also expected to be positively related to the transmission rate of certain parasites (Tompkins et al. 2002). High host population density may therefore lead to an increase in parasite abundance (Arneberg 2001).

In the present study, we made use of two comprehensive datasets to examine the relationship between infection by the parasitic gapeworm (*Syngamus trachea*) and individual variation in annual survival probability of house sparrows (*Passer domesticus*). Using multievent capture-mark-recapture modeling we examined variation in annual survival among house sparrows that were either infected or not. The infection status of hosts was determined both from collected samples of feces and observation of a symptoms of severe gapeworm infection, gasping for air. Even though it is known from domestic species that *S. trachea* may increase mortality (Permin and Hansen 1998), there are very few studies of its effect on wild populations. A study by Wissler and Halvorsen (1975) on harvested willow grouse (*Lagopus lagopus*) indicated that *S. trachea* may reduce host survival in northern

Norway. Loman (1980) also found that nestling hooded crows (*Corvus cornix*) showing gapeworm sickness symptoms 24 days after hatching had a significantly lower chance of surviving the summer. To our knowledge, ours is the first study to assess the relationship between survival and infection of *S. trachea* based on feces sampling from wild populations.

Materials and methods

Study area

The study was carried out in an archipelago consisting of 18 islands covering ca. 1600 km^2 in the Helgeland district in northern Norway (Supplementary material Appendix 1). The house sparrows on these islands have been systematically captured, marked and reencountered several times during their lifetime since 1993 (e.g. Sæther et al. 1999, Ringsby et al. 2002, Jensen et al. 2008). In this study we apply the term "reencounter" instead of "recapture" because birds were detected after being marked and released either by recapture or resighting of unique band combinations (more below). We focused on 4 of the study islands (Aldra, Gjerøy, Hestmannøy and Indre Kvarøy). Within two of the four islands (Hestmannøy and Gjærøy), the local population of house sparrows is naturally divided into northern and southern components which we assume to be separate populations as they are separated by more than 4 kilometers of agricultural, meadow and forest land and dispersal between the populations has been rare (Myhre et al., unpubl.). Accordingly, we included 6 subpopulations, distributed among 4 islands, in our models. On these islands a high proportion of individuals have been individually marked (> 90%). Symptoms of gapeworm infection (gasping for air, a sign of severe infection) have been collected since 2004, and feces samples used for egg counts have been collected since 2007 (see below). Because of the sedentary nature of the house sparrows, the large size of the total study area, the high reencounter probability and the high proportion of individually marked birds in our metapopulation, we can identify the majority of individuals that moves between islands in the study area (Pärn et al. 2009, 2012) and distinguish mortality from dispersal unless individuals leave the study area or are captured without a mark.

Study species

The parasite of interest in this study is the nematode worm *S. trachea*. *S. trachea* has a cosmopolitan distribution and has been found in most terrestrial bird genera (Yamaguti 1961). The parasite is known as “gapeworm” in the domestic bird industry, where outbreaks have caused substantial problems (Atkinson et al. 2008). *S. trachea* has a lifecycle that may include one paratenic host (i.e. not necessary for development) in addition to the final bird host. These Intermediates can be earthworms, snails or insects (Atkinson et al. 2008). After ingestion by a bird, larvae make their way from the stomach of the bird through the blood vascular system to the lungs or trachea, where they grow into adults and then permanently attach to a mate (Atkinson et al. 2008). The adult male parasite is 3-5 mm long and the adult female is 17-30 mm long (Barus and Blazek 1965). After a female and male are joined, the female releases eggs which are coughed up by the host ,swallowed, and passed out through feces (Atkinson et al. 2008). The lifespan of adult *S. trachea* in domestic chickens (*Gallus gallus domesticus*) has been reported as 2 – 4 months. The adult parasite feeds on blood in the trachea tissue causing mechanical damage, anemia, inflammation and excess mucus production. The birds that are severely infected may develop symptoms consisting of gasping, wheezing and shaking of the head. This discomfort may affect food uptake, and combined with the blood loss, may cause death (Atkinson et al. 2008).

The house sparrow is a small passerine with a global distribution (Anderson 2006). The house sparrows live in close association with human settlements, in particular dairy farms. House sparrows over-wintering on dairy farms forage on cattle food and seeds from cultivated crops (Anderson 2006). In summer, house sparrows feed, to a large extent, on different types of seeds and insects (Anderson 2006). House sparrows shelter inside farm buildings when the weather is harsh, especially in winter (Summers-Smith 1988). Survival probability of house sparrows may vary between years, populations and age classes (Ringsby et al. 1999) but is generally found to be low (especially for juveniles). This means that even if individuals survive their first winter (i.e. become adults), few survive more than 2 years (Anderson 2006). Houses sparrows can become exposed to *S. trachea* infection (mainly during the summer/autumn, Holand et al. 2013) through oral ingestion of parasite larvae (e.g. contaminated food items) (Atkinson et al. 2008).

Field work and sampling

Adult and juvenile house sparrows were captured using mist-nets. Once marked, individuals were identified at a distance by the unique combinations of color rings on their tarsi. Following capture, we measured right tarsus length and body mass. We accounted for measurement variation among fieldworkers by obtaining the relationship between each fieldworker and the most experienced fieldworker using general linear regression techniques (see Ringsby et al. 2002, Jensen et al. 2008, Pärn et al. 2009, for detailed description of field work). Feces samples were collected and symptom status was noted when birds were captured. Feces samples were collected by placing the bird in a paper bag with a small hole at the top to prevent asphyxiation. Feces was removed from the bag and the number of *S. trachea* eggs were then counted under a microscope using egg flotation techniques. For detailed description of feces sample collection and analysis, see Holand et al. (2013). To avoid bias in survival estimates (Anderson et al. 1994), we included only individuals that had been initially captured as juveniles (i.e. all encounter histories started when the bird was juvenile). Our first dataset consisted of encounter histories from 603 individuals that provided 1019 feces samples collected during the summer and autumn of 2007 – 2011 (01 May – 25 Oct). Our second dataset consisted of encounter histories from 1391 individuals that provided 3362 observations of symptom (gasping for air) status during the summer and autumn of 2004 – 2011 (01 May – 25 Oct).

We estimated a body condition index (BC) as the unstandardized residuals (see Schulte-Hostedde et al. 2005, and references therein) obtained by regressing body mass on tarsus length with a linear model (all years and islands pooled). BC was estimated separately for juveniles, adult males and adult females since morphology may differ significantly between the groups (Jensen et al. 2004). Male and female juveniles were pooled due to difficulties in determining sex based on plumage. BC provides an index of the deviance in body mass from the average of the population accounting for skeleton size as a continuous variable..

We applied a standardized annual estimate of relative population size (see supplementary materials in Hansen et al. 2013) that was obtained by calculating the standard z-score (subtracting mean and dividing by standard deviation) of population size estimates within 6 sub-populations among the 4 islands. This would correspond to a population density (PD) within each sub-population in the period 2004 - 2011. BC and PD were used as continuous covariates in our mark-recapture models (more below).

Observed symptoms and number of *S. trachea* eggs

In the years 2007-2011, we had data on both number of eggs in feces and symptom status ($n = 2396$). We tested the repeatability of our counting procedure by regressing the first count on the second count from 20 samples. The coefficient of determination (r^2) from the regression was estimated to be 0.97 ($F = 12.14$, $df = 38$, $P = 0.001$). In order to test whether individuals with visible symptoms also had a higher number of eggs in feces, we ran a generalized linear model (glm procedure, R version 2.15.3; R Core Team 2013) with symptoms (yes/no) as the response variable and number eggs as the explanatory variable.

Capture-Mark-Recapture Analyses

We used a type of multievent capture-mark-recapture model (more below)to estimate annual survival of birds in our study population separately for each dataset. We defined two states in our models. In the analysis of dataset one, states were infected/not infected; for dataset two, symptomatic/non-symptomatic. Birds could be classified as one of these states when recaptured. However, state was uncertain ("unknown") for resighted birds. For these birds, state allocation was determined using a probabilistic framework implemented in our multievent models (more below). This means that an individual could be recorded as not infected (state = 1), infected (state = 2), not recorded (0), or only resighted (3) in a given year. For example, the individual capture history “1 3 2 0” from dataset one indicated that the individual was recorded as not infected the first year, recorded as alive but not caught in the second year (state uncertain), recorded as infected the third year and not recorded at all in the fourth year. Below we refer to state (3) as an "unknown" state because birds in this state may be infected or not infected (dataset 1); not symptomatic or symptomatic (dataset 2). To account for state uncertainty when birds were resighted, we used a type of multievent state-uncertainty model, hidden Markov model (HMM), proposed and developed by Conn and Cooch (). Parameters in this model are S_t^s, p_t^s, Ψ_t^{ab} , δ_t^s and π_t^s where S_t^s is the probability that an individual in state *s* at time *t* survives to time *t* + 1 and does not emigrate from the study area; p_t^s is the probability that an individual in state *s* at time *t* is encountered at time *t*; Ψ_t^{ab} is the probability that an individual in state *a* at time *t* will be in state *b* at time *t* + 1 given that it survives to *t* + 1; δ_t^s is the probability that the state of an animal is observed given that it is in state *s* at time *t* and encountered at time *t*; and π_t^s is the probability that an animal originally encountered at time *t* is in state *s* (for more details, see Conn and Cooch 2009).

We used the model fitting options provided in WinBUGS (Lunn et al. 2000) through the interface of R version 2.15.3 (R Core Team 2013, package R2WinBUGS version 2.1 – 18) to perform our analyses. WinBUGS uses MCMC simulations to obtain a Bayesian posterior stationary distribution of parameters in a given model (Kéry and Schaub 2011). For each model that we considered we used 3 chains each with 10 000 iterations and a thinning rate of 3; the first 5000 iterations were discarded ("burn in"). Mixing and convergence of chains to a stationary distribution was evaluated by visual inspection of time-series plots produced by WinBUGS (Kéry and Schaub 2011) and the Brooks-Gelman-Rubin criterion (*R-hat*, Brooks and Gelman 1998). We applied vague priors for variables with normal (N (0, 1000)) and uniform (0, 1) distribution.

We included the additive covariates of age (juvenile/adult), body condition and population density in the survival component of all our models. Significant differences in survival probability between juveniles and adults have been documented previously in the study system (Ringsby et al. 1998, 1999). Body condition has been shown to correlate with individual survival probability in several passerine species (e.g. Hochachka and Smith 1991, Magrath 1991, Ringsby et al. 1998, Both et al. 1999, Naef-Daenzer et al. 2001). Population density has also been shown to correlate with individual survival probability of several bird species (for review see Newton 1998). While maintaining these covariates in our models, we also investigated the relationship of island (Aldra, Gjerøy, Hestmannøy and Indre Kvarøy), year, and their interaction, with survival and reencounter probability. We did not include state in the survival or reencounter components during the model selection (see below). δ, π and Ψ were kept constant in all models (i.e. we assumed no differences with covariates).

We considered parameter estimates (e.g. survival probability of groups) in our models as significantly different if the Bayesian 95% credibility interval (CI) of the posterior distribution of their difference (Delta) did not include zero. This is analogous to the "corner point parameterization" in generalized linear models (see Dobson and Barnett 2008) where group estimates are defined as differences from a reference category (e.g. the intercept) and estimates of the slopes of continuous variables are considered significant if different from zero (i.e. CI does not include zero). This parameterization can be readily formulated in WinBUGS (Kéry and Schaub 2011).

For model selection, we applied the deviance information criteria (DIC) which assesses the fit of a model based on the posterior mean deviance ($\bar{D}$) and effective number of parameters (p_D) (Spiegelhalter et al. 2002). We are aware that the effectiveness of DIC for model selection has been a topic of discussion (Kéry and Schaub 2011). However, DIC values have been used for model selection in several studies (e.g. Guo and Carlin 2004, Papadatou et al. 2012, Youdom et al. 2012) and the performance of DIC in model selection has also received support in simulation studies where the underlying (true) model was known (see Wilberg and Bence 2008, and references therein). Nonetheless, we also investigated parameter estimates and posterior distributions in order to evaluate a model's explanatory ability.

Protocol of analyses

As the potential differences between years and islands may have been explained by differences in survival and/or reencounter probabilities, we ran a set of candidate models which included year and island either together, separately or in interaction in the survival and/or reencounter part of the model (Table 1 and 2). The model that obtained the lowest DIC value was then used to investigate the relationships between survival and infection status either measured as eggs found in feces or symptom status. We started this investigation by first including state in the survival and reencounter part of the model as an additive covariate. We subsequently added interactions with other covariates in the survival component of the model. Interactions were investigated separately in separate models and finally in a "full" model with all interactions present in the survival component of the model (Supplementary material Appendix 2).

Results

Visible Symptoms and *S. trachea* eggs in feces

The generalized linear model analysis revealed a significant difference in number of *S. trachea* eggs in feces between individuals exhibiting symptoms and those that did not exhibit such symptoms ($\chi^2 = 71.09$, $d.f. = 1$, $P < 0.001$). Symptomatic individuals had on average a higher number of eggs in their feces samples compared to non-symptomatic individuals (Fig. 1). Over the period 2007 – 2011 77.08 % of feces samples taken from juveniles with symptoms ($n = 49$) and 82.50 % of feces samples from adults with symptoms ($n = 41$) contained eggs of *S. trachea*. 80.94% of individuals with parasite eggs in the feces did not have visible symptoms of disease.

Survival and *S. trachea* eggs in feces

For the 2007-2011 dataset the top model (lowest DIC value) contained only the relationship of year with reencounter probability (Table 1). The top model also included a significant and positive relationship of body condition index with survival probability (BC = 0.13, CI = (0.07, 0.19)); and indicated a significant decline in survival probability with increasing population density (PD = - 0.27, CI = (- 0.47, - 0.08)). Despite age being in the top model, the difference in survival between juveniles and adults was not significant (Delta $_{S(A) - S(J)}$ = 0.07, CI = (- 0.01, 0.15)).

We added the relationship between infection (infected/not infected) to the reencounter and survival components of the top model. The difference in reencounter probability for infected/not infected house sparrows was not significant (Delta $_{p(1)- p(2)}$ = 0.30, CI = (- 0.08, 0.68)); neither was the difference for survival for these two states (Delta $_{S(1) - S(2)}$ = - 0.06, CI = (- 0.16, 0.04)). The interaction term between age classes and infection status revealed no significant difference for either juveniles (Delta $_{S(J1) - S(J2)}$ = - 0.06, CI = (- 0.16, 0.05)) or adults (Delta $_{\mathrm{s}(A1) - S(A2)}$ = - 0.10, CI = (- 0.33, 0.19)). Furthermore, there was no significant difference in the relationship of BC (Delta $_{S(BC1) - S(BC2)}$ = - 0.15, CI = (- 0.34, 0.03)) or population density (Delta $_{S(PD1) - S(PD2)}$ = 0.28, CI = (- 0.26, 0.85)) with survival probability between non-infected and infected individuals, respectively (Supplementary material Appendix 2, Table B1).

Survival and symptoms of infection

For the 2004 – 2011 dataset, the highest ranked model contained the additive covariates of both islands and years with reencounter probability. The survival part of this model contained the relationship with island (Table 2). Estimates from this model revealed a significant difference in survival probability between juveniles and adults (Delta $_{S(A) - S(J)}$ = 0.05, CI =

(0.01, 0.10)); a significant positive relationship of body condition (*BC* = 0.08, CI = (0.04, 0.11)); and a significant negative relationship of population density (*PD* = - 0.16, CI = (- 0.28, - 0.05)). When we added symptom status to the top model we found a significant difference in mean reencounter probability (Delta $_{p(1)-p(2)}$ = 0.35, BCI = (0.27, 0.42)) between individuals showing symptoms of severe infection and those that did not show such symptoms. We also found a significantly lower mean survival probability (Delta $_{S(1)-S(2)}$ = 0.16, CI = (0.09, 0.23)) for symptomatic individuals compared to non-symptomatic individuals. Estimates suggested no significant difference (Delta $_{S(J1)-S(J2)}$ = - 0.01, CI = (- 0.16, 0.13)) in survival probability between non-symptomatic and symptomatic juveniles; and a significant difference (Delta $_{S(A1)-S(A2)}$ = 0.23, CI = (0.15, 0.32)) in survival probability between non-symptomatic and symptomatic adults. Symptomatic adults had a lower survival probability compared to non-symptomatic adults (Fig. 2). We found no significant difference in the relationship between body condition (Delta $_{S(BC1)-S(BC2)}$ = 0.09, CI = (- 0.02, 0.20)), population density (Delta $_{S(PD1)-S(PD2)}$ = - 0.27, CI = (- 0.58, 0.05)) or islands with survival probability between non-symptomatic and symptomatic individuals (Supplementary material Appendix 2, Table B2).

Discussion

Based on data from an insular metapopulation of house sparrows off the coast of Helgeland in northern Norway, our results suggest that adult house sparrows carrying obvious symptoms (gasping behavior) of severe infection by the parasite *S. trachea* had reduced annual survival compared to local conspecifics that showed no observable signs of infection (no gasping). This suggests that the presence of *S. trachea* may have a negative effect on individual lifetime reproductive success in the sampled host populations through its relationship with individual lifespan (). In contrast, we found no statistically significant differences in annual survival probability between symptomatic and non-symptomatic juveniles, and infected and non-infected adults or juveniles based on presence/absence of *S. trachea* eggs in host feces.

The reason why analyses using infection status obtained by feces examination failed to find a relationship with survival probability may be due to several factors. The most obvious hypothesis is that only the most severely infected individuals suffer a reduced probability to survive to the next year and these are few in number in the host population in our study area. If moderate cases of infection also suffered lower survival or severe infection was more widespread then we would likely have found a difference in survival between infected and non-infected house sparrows in our study. In order to evaluate our hypothesis, the only reliable and practical way of determining the severity of an infection is by counting the number of adult *S. trachea* inhabiting a house sparrow is *post mortem* examinations. This was not an option for this non-invasive long-term study. This leaves us with the number of eggs found in feces as a possible proxy which may be positively correlated with the number of parasites and/or the severity of infection. Such positive correlations between number of adult parasites and eggs found in feces have been reported for the parasite *Trichostrongylus tenuis* in red grouse (*Lagopus lagopus scoticus*, Shaw and Moss 1989), strongyle parasites in soay sheep (*Ovis aries*, Clutton-Brock and Pemberton 2004) and *Heterakis gallinarum* in chickens (*Gallus gallus domesticus*, Das et al. 2011). To our knowledge, no such study has been done with *S. trachea*. However, the present study has revealed a positive relationship between the number of eggs found in feces and obvious symptoms of infection (Fig. 1). Whether or not the number of eggs is the direct cause of the symptoms (as an irritant in the respiratory system) or an indicator of the number of egg-producing adult parasites should be topics for further study. A relationship between the number of eggs/larvae found in feces and survival has been reported in other host and parasite species (Festa Bianchet 1991, Coltman et al. 1999). A direct investigation of this relationship would require expansion of the HMM to estimate fecal egg count in addition to the state of an individual. This extended feature is currently not available, but should be developed for future studies.

We found a substantially lower reencounter probability of individuals exhibiting symptoms of severe infection compared to individuals not exhibiting such symptoms (Supplementary material Appendix 2, Table B2). This may be caused by a reduced level of activity due to respiratory distress or a general lack of energy. Apathy has been reported in individuals infected with *S. trachea* in domestic bird species (de Wit 1995). One may expect a highly active individual to have a higher probability of both encountering our mist nets and being observed and identified by the combination of rings on its tarsi. This difference in reencounter probability between symptomatic and non-symptomatic individuals may underline the severe effect of the symptoms. Similar differences in reencounter probability have been detected in other parasite and host species (Retallick et al. 2004, Lachish et al. 2011).

We did not find a difference in survival probability between symptomatic and non-symptomatic juveniles. This may be due to the relatively low annual survival probability of juveniles in general (Appendix 2 and Ringsby et al. 1998, 1999). Therefore, a reduction in survival caused by infection of *S. trachea* may be very difficult to detect without relatively large sample sizes. We also found that only 77.08 % of juveniles showing symptoms of severe infection had feces samples containing eggs of *S. trachea* in their feces (2007-2011 dataset) which implies that we may have misclassified some uninfected birds as infected (this would increase survival for 'infected' birds in our models).. If a bird experiences a high level of stress when captured then ensuing symptoms of that stress may be misinterpreted by an inexperienced fieldworker as being the gasping symptoms of severely infected individuals.

Alternatively, the bird may indeed be infected but show no signs because the parasites have not started to produce eggs at time of capture. Detection of *S. trachea* eggs in feces after parasite maturity has been shown to be remarkably reliable (Barus 1966a, b, HH, HJ, HP, BES, THR, unpubl.).

We found that adult survival of symptomatic individuals was significantly lower compared to non-symptomatic adult individuals (see Fig. 2). A higher classification success may be due to highly visible distress and breathing difficulties that can be quite severe in adult house sparrows (personal observation). As mentioned above, Loman (1980) found a negative relationship between fledgling survival and symptoms of *S. trachea*. This pattern appears to be different from the one found in this study (effect on adults only). Since Loman (1980) did not investigate the relationship between survival of adult hooded crows and symptoms, we do not know if our pattern with adult survival was present in his population. However, one may have expected that the same pattern should be present in juvenile survival. One possible explanation for the difference may be caused by a difference between uncertainty of symptoms in our study of juveniles (77.08 %) and in Loman (1980). Nonetheless, analyses only using gapeworm sickness as a sign of infection will in most cases overlook the majority of infected individuals as many individuals with parasite eggs in the feces did not have visible symptoms of disease caused by *S. trachea* (80.94%). Using symptoms can thus give an under-exaggerated picture of the "general" effect of *S. trachea* on its hosts. Analyses using data from feces examinations are more consistent with prevalence but this technique faces the challenge of estimating the severity of the infection. Another difference between the two datasets applied in the study was that the dataset on observed symptoms included three additional years of data compared to the dataset on collected feces samples. If a strong temporal effect of infection on survival was present during the years 2004-2006, this effect would be expressed in the results from the dataset on observed symptoms (2004-2011), but not in the results from the dataset on collected feces samples (2007-2011), which may thus have contributed to the difference in results in analyses of the two datasets. Caution should be taken in interpreting results between "similar" analyses when the datasets are of different lengths and sample sizes. Indeed, such effects may have been the explanation for why the highest ranked models for reencounter and survival probabilities differed between the two datasets (see Table 1 and 2).

In addition to the possible effect of *S. trachea*, interactions between one or more parasites may also contribute to variation in survival in house sparrows. We have detected several other parasite species inhabiting our study populations (Holand et al. 2013), both from our feces samples (endoparasites: *Isospora spp.*, *Capillaria spp*., *Choanotaenia spp.*) and visual inspection of house sparrows (ectoparasites: *Hippoboscidae spp.*, *Ornithonyssus spp.*, *Ceratophyllus spp*.). The combined effects among these parasite species and *S. trachea* on fitness among house sparrows are not presently known.

This study has shown that parasites may have the ability to reduce the survival probability of severely infected adult hosts in natural populations of a short lived host species. Life span has been shown to influence life time reproductive success of individuals in such populations (Jensen et al. 2004) and is also an important factor affecting the population growth rate of short lived species (Sæther et al. 1999). However, our study also shows that the majority of infected hosts may not suffer a significant parasite induced reduction in survival probability. Furthermore, we found a significant difference in reencounter probability between sick and healthy individuals. This illustrates the importance of carefully modeling detection probability to avoid reporting biased estimates of survival. Due to the natural aggregation of parasites in host populations their effects may often be underestimated (Anderson 1995). Understanding the effect of parasites on host fitness may be crucial to our understanding of host species population dynamics (Hudson et al. 1998, Albon et al. 2002, Pedersen and Greives 2008).

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Figure legends

Fig. 1 Observations of Gapeworm sickness symptom status (1 = yes, 0 = no) and number of *Syngamus trachea* eggs counted in feces in the years 2007-2011 in a metapopulation of house sparrows on 4 islands at the coast of Helgeland, northern Norway (*n* = 2396). Line created by logistic regression based on a generalized linear model with symptoms (1/0) as the response variable and number of eggs as the only explanatory variable

Fig. 2 Estimated mean survival probability (*S*) of juvenile and adult house sparrows which were observed as non-symptomatic and symptomatic for gapeworm sickness, respectively, in the years 2004 – 2011 on 4 islands at the coast of Helgeland, northern Norway. Lines indicates upper and lower limit of a 95 % Bayesian credibility interval of the mean value. For model details, see Material and Methods and Supplementary material Appendix 2

Tables

Table 1: Set of ecologically relevant candidate models for the annual survival probability (Logit (*S*)) and reencounter probability (Logit (*p*)) of house sparrows in parasite infection data from feces samples collected from a metapopulation on the coast of Helgeland in northern Norway. Data was collected on 4 islands during in the years 2007-2011. Where *AGECLASS* is a factor with the two levels: adult/juvenile, *BC* is individual body condition (continuous) and *PD* is population density (continuous). The highest ranked model according to the DIC criteria was chosen for further analyses. The effective number of parameters (p_D) and difference in DIC values compared to the highest ranked model (Δ DIC) is shown for each model. Components for δ, π and Ψ were kept constant in all models. Interaction terms between two variables are denoted A × B. Note that models with interactions also include the main effects of A and B.

Model no.	Survival component	Reencounter component	p_D	Δ DIC
1	*AGECLASS + BC + PD*	*YEAR*	431.22	0
2	*AGECLASS + BC + PD*	*ISLAND + YEAR*	425.26	6.99
3	*AGECLASS + BC + PD + ISLAND*	*YEAR*	452.14	35.00
4	*AGECLASS + BC + PD*	*ISLAND x YEAR*	435.41	46.75
5	*AGECLASS + BC + PD + ISLAND*	*ISLAND + YEAR*	463.06	58.31
6	*AGECLASS + BC + PD + ISLAND*	*ISLAND x YEAR*	642.55	275.95
7	*AGECLASS + BC + PD*	*ISLAND*	761.73	413.25
8	*AGECLASS + BC + PD*	*(intercept only)*	835.50	481.50
9	*AGECLASS + BC + PD + ISLAND*	*ISLAND*	820.18	488.96
10	*AGECLASS + BC + PD + ISLAND*	*(intercept only)*	835.63	495.16
11	*AGECLASS + BC + PD + YEAR*	*ISLAND*	1260.13	989.55

12	*AGECLASS + BC + PD + YEAR*	*(intercept only)*	1410.99	1134.13
13	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND*	1444.74	1193.14
14	*AGECLASS + BC + PD + ISLAND + YEAR*	*(intercept only)*	1506.28	1251.00
15	*AGECLASS + BC + PD + ISLAND x YEAR*	*(intercept only)*	1754.51	1554.50
16	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND*	1827.91	1664.77
17	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND + YEAR*	1750.83	1751.77
18	*AGECLASS + BC + PD + ISLAND + YEAR*	*YEAR*	3222.41	3184.43
19	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND + YEAR*	3297.61	3294.07
20	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND x YEAR*	5342.52	5270.86
21	*AGECLASS + BC + PD + ISLAND x YEAR*	*YEAR*	5654.37	5661.09
22	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND x YEAR*	5761.50	5679.19
23	*AGECLASS + BC + PD + YEAR*	*YEAR*	7594.30	7483.50
24	*AGECLASS + BC + PD + YEAR*	*ISLAND x YEAR*	9730.15	9488.70
25	*AGECLASS + BC + PD + YEAR*	*ISLAND + YEAR*	11565.73	11299.60

Table 2: Set of ecologically relevant candidate models for the annual survival probability (Logit (*S*)) and reencounter probability (Logit (*p*)) of house sparrows in parasite symptom data collected from a metapopulation on the coast of Helgeland in northern Norway. Data was collected on 4 islands during in the years 2004-2011. Where *AGECLASS* is a factor with the two levels: adult/juvenile, *BC* is individual body condition (continuous) and *PD* is population density (continuous). The highest ranked model according to the DIC criteria was chosen for further analyses. The effective number of parameters (p_D) and difference in DIC values compared to the highest ranked model (Δ DIC) is shown for each model. Components for δ, π and Ψ were kept constant in all models. Interaction terms between two variables are denoted A × B. Note that models with interactions also include the main effects of A and B.

Model no.	Survival component	Reencounter component	p_D	Δ DIC
1	*AGECLASS + BC + PD + ISLAND*	*ISLAND + YEAR*	1545.09	0
2	*AGECLASS + BC + PD*	*ISLAND + YEAR*	1596.03	36.09
3	*AGECLASS + BC + PD*	*YEAR*	1611.14	45.17
4	*AGECLASS + BC + PD + ISLAND*	*YEAR*	1622.43	69.30
5	*AGECLASS + BC + PD + ISLAND*	*ISLAND x YEAR*	1556.48	117.42
6	*AGECLASS + BC + PD*	*ISLAND x YEAR*	1667.28	202.29
7	*AGECLASS + BC + PD*	*ISLAND*	2066.44	658.15
8	*AGECLASS + BC + PD + ISLAND*	*ISLAND*	2100.85	705.97
9	*AGECLASS + BC + PD*	*(intercept only)*	2141.63	729.67
10	*AGECLASS + BC + PD + ISLAND*	*(intercept only)*	2182.88	784.39
11	*AGECLASS + BC + PD + YEAR*	*(intercept only)*	2721.28	1428.84
12	*AGECLASS + BC + PD + ISLAND + YEAR*	*YEAR*	2421.45	1473.48
13	*AGECLASS + BC + PD + YEAR*	*ISLAND*	2756.34	1474.42
14	*AGECLASS + BC + PD + ISLAND + YEAR*	*(intercept only)*	2809.28	1542.99

15	*AGECLASS + BC + PD + YEAR*	*YEAR*	2556.53	1592.06
16	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND + YEAR*	2542.28	1605.36
17	*AGECLASS + BC + PD + YEAR*	*ISLAND + YEAR*	2653.64	1677.84
18	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND*	2946.81	1685.21
19	*AGECLASS + BC + PD + ISLAND x YEAR*	*(intercept only)*	2982.10	1803.06
20	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND*	2981.12	1805.43
21	*AGECLASS + BC + PD + YEAR*	*ISLAND x YEAR*	10206.93	9124.74
22	*AGECLASS + BC + PD + ISLAND + YEAR*	*ISLAND x YEAR*	10316.67	9265.28
23	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND x YEAR*	12076.08	11035.12
24	*AGECLASS + BC + PD + ISLAND x YEAR*	*ISLAND + YEAR*	12187.48	11231.10
25	*AGECLASS + BC + PD + ISLAND x YEAR*	*YEAR*	22847.66	21801.33