CAMBRIDGE UNIVERSITY PRESS

Temporal and spatial variation in prevalence of the parasite Syngamus trachea in a metapopulation of House Sparrows (Passer domesticus).

Journal:	*Parasitology*
Manuscript ID:	PAR-2013-0026
Manuscript Type:	Research Article - Standard
Date Submitted by the Author:	23-Jan-2013
Complete List of Authors:	Holand, Håkon; NTNU, Department of Biology Jensen, Henrik; NTNU, Department of Biology Tufto, Jarle; NTNU, Department of Mathematical Sciences Sæther, Bernt-Erik; NTNU, Department of Biology Ringsby, Thor; NTNU, Department of Biology
Key Words:	Parasite, Syngamus trachea, House Sparrow, prevalence, metapopulation

SCHOLARONE™ Manuscripts

For Review

Full title: Temporal and spatial variation in prevalence of the parasite *Syngamus trachea* in a metapopulation of House Sparrows (*Passer domesticus*).

Short title: Parasite prevalence in House sparrows.

Håkon Holand[1] (H. Holand), Henrik Jensen[2] (H. Jensen), Jarle Tufto[3] (J. Tufto), Bernt-Erik Sæther[2] (B. E. Sæther) and Thor Harald Ringsby[2] (T. H. Ringsby).

[1] **Corresponding author** (**name:** Håkon Holand**, address:** Norwegian University of Science and Technology, Centre for Conservation Biology, Department of Biology , 7491 Trondheim, Norway, **Phone**: +4741645380, **email**: hakon.holand@bio.ntnu.no)

[2] Norwegian University of Science and Technology, Centre for Conservation Biology, Department of Biology , 7491 Trondheim, Norway.

[3] Norwegian University of Science and Technology, Centre for Conservation Biology, Department of Mathematical Sciences , 7491 Trondheim, Norway.

For Peer Review

SUMMARY

When investigating parasite-host dynamics in wild populations, a fundamental parameter to investigate is prevalence. This quantifies the percentage of individuals infected in the population. Investigating how prevalence changes over time and space can reveal interesting aspects in the parasite-host relationship in natural populations. We investigated the dynamic between a common avian parasite (*Syngamus trachea*) in a host metapopulation of House Sparrows (*Passer domesticus*) on the coast of Helgeland in northern Norway. We found that parasite prevalence varied in both time and space. In addition, the parasite prevalence was found to be different between demographic groups in the local populations. Our results reveal just how complex the dynamic between a host and its parasite may become in a fragmented landscape. The mechanisms causing this complexity are not fully understood, but needs to be further examined to understand how parasite-host interactions may affect the ecological and evolutionary dynamics and viability of host populations.

Key words: Parasite, Syngamus trachea, House Sparrow, prevalence, metapopulation.

For Peer Review

KEY FINDINGS

- Parasite prevalence can vary substantially in time and space in a metapopulation of wild hosts.
- Demographic groups of wild hosts may have different levels of parasite prevalence.
- Long term studies needed to reveal dynamic of parasite-host relationship.

INTRODUCTION

Understanding the temporal and spatial distribution of parasite populations within and across host populations is fundamental for understanding the possible impact the respective parasite(s) may have on the evolutionary dynamics as well as population dynamics of the host species (Hudson *et al.*, 2002). In addition, differences in parasite distributions among sub-groups in the host population can reveal important aspects of the parasite-host relationship (Hudson *et al.*, 2002; Gurski and Ebbert, 2003). Few empirical studies of parasite prevalence in vertebrate populations span over longer time periods (but see: Gulland *et al.*, 1993; Hudson *et al.*, 1998) and even fewer contain observations of temporal and spatial variations of prevalence in host metapopulations (Atkinson *et al.*, 2000; Vogeli *et al.*, 2011). Theoretical metapopulation models have shown that spatial fragmentation of a host population may increase the persistence of infective agents (Earn *et al.*, 1998) and that persistence of an infective agent is determined by a balance between spatial, demographic and epidemiological components (Jesse and Heesterbeek, 2011). Although a theoretical framework for modelling parasites in a metapopulation exists, there is a need for empirical datasets preferably stretching over as many subpopulations and time periods as possible (Hudson *et al.*, 2002). This need has become urgent due to an increase in number of fragmented populations as a result of human impact (Saunders *et al.*, 1991). In such a system, parasites may play an important role in conservation of endangered populations (Hess, 1996).

The parasite of interest in this study is the nematode worm *Syngamus trachea* (henceforth *S. trachea*). *S. trachea* has a cosmopolitan distribution and has been found in most terrestrial bird genera (Yamaguti, 1961). In Norway the parasite has been recorded in several wild bird species (for list see: Bakke, 1973). The parasite is known as “Gape worm” in the domestic bird industry, where outbreaks have caused substantial problems (Atkinson *et al.*, 2008). *S. trachea* has a lifecycle that may include one intermediate vector host in addition to the final avian host. These intermediates can be earthworms, snails or insects (Atkinson *et al.*,

For Peer Review

2008). By eating one or more of these intermediate hosts containing an egg or larvae of *S. trachea*, the bird can become infected (Clapham, 1934). The larva makes its way from the stomach of the bird, through the blood vascular system to the lungs or trachea, where it then grows into an adult and finds a mate to copulate with (Atkinson *et al.*, 2008). The prepatent period in chickens (*Gallus gallus*) is 12-17 days and the adults can live 2-4 months (Barus, 1966b). After a female and male are joined, they mate and the female releases eggs which are coughed up by the host and then swallowed (Atkinson *et al.*, 2008). The eggs then pass out in the faeces and may enter another bird either directly or via an intermediate host (Clapham, 1934; Bakke, 1973). The adult male parasite is 3-5 mm long and the adult female is 17-30 mm long (Barus and Blazek, 1965). After copulation the adult male and female are permanently attached to each other in a Y-shape. The parasites feed on blood in the trachea tissue causing mechanical damage, anaemia, inflammation and excess mucus production. The birds that are 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 bird with a global distribution, and is widely spread on the Northern hemisphere (Anderson, 2006). The House Sparrows along the coast of northern Norway live in close association with human settlements, in particular dairy farms. This is strongly reflected in the behaviour ecology and foraging patterns of the species. During the winter a substantial part of the diet consists of concentrated cattle food, and seeds from cultivated crops (Anderson, 2006). In the summer season the House Sparrows forage outdoors, to a large extent, on different types of seeds and insects (Anderson, 2006). Sparrows living on farms most frequently place their nests inside cowsheds and barns. House Sparrows also shelter inside farm buildings when the weather is harsh (especially in winter) (Summers-Smith 1988). Because of the species' sedentary nature and the high proportion of individually recognizable birds in our metapopulation, we have the opportunity to track individual movement between islands in the study area (Pärn *et al.*, 2009; Pärn *et al.*, 2012).

In the present study we explore the prevalence of the parasite *S. trachea* in a metapopulation of House Sparrows (*Passer domesticus*) in the Helgeland archipelago in northern Norway over a 4-year period. This is a metapopulation that has been thoroughly studied at an individual based level since 1993 and offers a unique opportunity to shed light on parasite-ecology in a spatially distributed population of wild hosts. Our aim was to investigate whether the prevalence of *S. trachea* varied in time and/or space on the respective

For Peer Review

islands. We also investigated the possibility that prevalence patterns could be explained by differences among the demographic groups in the respective populations.

For Peer Review

METHODS

Study area

The study was carried out in an archipelago consisting of 18 islands in the Helgeland district in northern Norway. The House Sparrows on these islands have been studied on an individual based level by capture-mark-recapture methods since 1993 (e.g Sæther *et al.*, 1999; Ringsby *et al.*, 2002; Jensen *et al.*, 2008). In this study we focus on 4 of the main study islands (Aldra, Gjerøy, Hestmannøy and Indre Kvarøy). On these islands a high proportion of the individuals have been individually marked (>90%), the annual recapture probability is high (>0.7, see Billing *et al.*, 2012), and faecal samples have been collected since 2007. These are islands where the birds live mainly in connection with farms. House Sparrows have been captured, marked and sampled several times during their lifetime.

Sample collection and analysis

During field work House Sparrows were captured using mist-nets. For the purpose of obtaining a faecal sample they were thereafter placed in paper bags with a small hole at the top to prevent asphyxiation. After approximately 10 to 15 minutes in the paper bag, a faecal sample had usually been obtained. According to procedures described in (Gjerde, 2007) each faecal sample was placed in 1 ml of MilliQ H_2O in a 1.5 ml cryo-tube. Samples were then kept refrigerated (at between 1 and 8 °C) until analysed. 1150 faecal samples were collected during the breeding seasons 2007 – 2010 (1^{st} May – 15^{th} August) from 752 birds. In addition, we also collected samples from one of the study islands (Hestmannøy) in the winters (February-March) of 2009 (32 samples) and 2010 (46 samples).

To individually mark each bird, they were assigned unique individual ring codes consisting of a numbered metal ring and three additional plastic colour rings; two rings on each tarsus. In this way individual birds could later be identified by observation/capture to determine e.g. age and dispersal distance. When captured, the sex was determined for adult birds based on plumage characteristics. Individuals were also categorized into juveniles (birds younger than one year) and adults (birds in their first breeding season or older). (See Ringsby *et al.* 2002; Jensen *et al.*, 2008; Pärn *et al.*, 2009, for further description of field work)

To analyse parasite load the faecal samples were first centrifuged at 3000 rpm for 60 sec. The supernatant of MilliQ H_2O was then removed and replaced with sucrose-saturated

For Peer Review

water. The samples were centrifuged again at 1500 rpm for 45 sec, and placed in a Mcmaster/Whitlock counting chamber under a microscope (Leica, model: DMLS). The number of *S. trachea* eggs were counted by eye using a handheld Redington Counter. Detection of eggs from *S. trachea* in bird faeces has been shown to be a reliable and stable way of monitoring infection in populations (Barus, 1966b; Barus, 1966c).

Statistical analyses

The response variable used in our statistical analyses was infection status. If eggs of *S. trachea* were found in a faecal sample the individual's infection status was defined as 1 (i.e."infected"). Correspondingly, if eggs were not detected in the faeces the individual was given an infection status of 0 (i.e. zero eggs).

Island was the only spatial explanatory variable used in the analyses. Temporal explanatory variables were year and seasonal day number (SDN). SDN indicated which day during the season a bird was sampled, where day 1 was set to 1st of May. The SDN variable was then centred on zero (mean = 0) in order to increase interpretability of possible interactions (Aiken and West, 1991).

Demographic explanatory variables consisted of age-class (adult/juveniles) and life-stage group (LSG: juvenile, adult male, adult female). We were not able to include sex of juveniles in the study due to difficulties in confidently determining sex of birds that had not acquired their adult plumage.

All analyses were done using the statistical software package R version 2.14.1 (R Development Core Team 2012). We applied generalized linear mixed models (package glmmADMB version 0.7.2.5) with a Bernoulli response variable and a logit link function in our investigation of prevalence. Because some birds (N=213) were caught more than once during a respective season we used individual identity as a random factor in order to avoid pseudoreplication.

To evaluate the effect of our explanatory variables we applied multiple model comparisons using an information-theoretic approach based on Akaike information criterion corrected for small sample sizes (AICc), which penalizes models with a high number of parameters relative to sample size (Burnham and Anderson, 2002).

In all our models we included the first order term of SDN due to the *a priori* assumption that prevalence of *S.trachea* varied significantly within years (Barus, 1966c). All models were created manually and explored all possible 2 way interactions between

For Peer Review

explanatory variables. We separated our analysis into two sections in order to reduce the number of potential models. In the first section, we ran a set of models that included all our spatial and temporal explanatory variables (SDN, year and island). The best model according to AICc was then used as the base model in the second section of analyses. In the second section of analyses, we investigated if demographic variables such as age-class and LSG could further improve the fit of the best model selected in the first section of analyses. Because the two demographic variables (age-classes and LSG) contained much of the same information, they were not included in the same models.

When including a random effect u representing heterogeneity between individuals the prevalence p becomes a random variable. For a given value of the random effect u (e.g. within a given individual), the relationship between the prevalence p and covariates X of interests becomes: $p = \text{logit}^{-1}(X\beta + u)$. Here our interest, however, is in the relationship between mean prevalence p of a randomly selected individual and the covariates X, which is given by

$$E(p) = \int \text{logit}^{-1}(X\beta + u)\, f(u) du,$$

where $f(u)$ is the density function of the random effect u.(Agresti, 2002, p. 498). This relationship (sometimes referred to as the marginal model) has a considerably shallower slope than the relationship between p and X conditional on u (the conditional model, see (Agresti, 2002), section 12.2.2 for an in-depth discussion). We computed the above integral using adaptive quadrature numerical integration (function integrate in R).

For Peer Review

RESULTS

First section of analyses

When analysing whether the prevalence of *S. trachea* was influenced by spatial and temporal variables the model comparisons (Table 1) showed that the model which received most support given the data included all the main effects of all the explanatory variables (island, SDN, SDN^2 and year), along with the interactions year × SDN, island × SDN, island × SDN^2 and island × year (see Appendix 1 for details). This model had an AICc value of 866.94 which was 4.27 lower than the second best model, suggesting that the highest ranked model was considerably better than the second best model. In addition, the AICc weight of the highest ranked model indicated that there was an 88.21 % probability that this model was the best given the data and the set of candidate models. The highest ranked model showed that a general difference in prevalence existed both between and within years and between and within islands (see Fig. 1).

The inclusion of the second order term of SDN as a main effect in the highest ranked model, pointed to a seasonal peak of prevalence within years on our islands. The mean prevalence appeared to increase during the breeding season to a general maximum in late summer and then decline towards autumn (see Fig. 1). Samples taken from Hestmannøy in the winters of 2009 (N=32) and 2010 (N=46) indicated a prevalence of only 3% and 0%, respectively, which strongly suggest that a seasonal peak pattern in the prevalence of *S. trachea* was present.

The main effect of year, showed an overall difference in prevalence between years (see Fig. 1). The main effect of islands indicated that the mean prevalence in the total sampling period was highest on Aldra and lowest on Gjerøy (see Fig. 1).

The interactions between the first order term of SDN and year/island (Table 1) suggested that the rate of change in prevalence with SDN differed both among years and islands, respectively. In addition, the interaction between the second order term of SDN and island (Table 1) points to a difference in date for the "peak" prevalence between islands (see Fig. 1).

The interaction between island and year indicated that the yearly change in prevalence was not the same on all islands. For example, at Hestmannøy the mean prevalence decreased successively each year, while on Aldra the mean prevalence decreased from 2007 to 2009 and then increased in 2010 compared to previous years (see Fig. 1).

For Peer Review

Second section of analyses

The extension of the highest ranked model from our first section of analyses by inclusion of demographic variables resulted in an improvement of the model (see Table 2). Here, the highest ranked model (see Appendix 2 for details) had an AICc value of 849.07 which was only 0.96 lower than the second best model (Table 2). This suggests that also the second best model should be viewed as a good model when interpreting the results. Accordingly, the AICc weights strongly supported the explanative properties of the two highest ranked models (Table 2). The highest ranked model from our first section of analyses obtained an AICc value which was 17.86 higher than the new highest ranking model, given the data and the alternative models.

The two highest ranked models in the second section of analyses included the main effects of LSG, year and island along with the interactions LSG × year and LSG × island. The highest ranked model also contained the interaction LSG × SDN^2. The main effect of LSG suggested differences in prevalence between the 3 life-stage groups. In general, juveniles appeared to have the highest mean prevalence and adult males the lowest (see Fig. 2). The interaction terms indicated that these differences were not the same between years or islands, and suggested that the peak date in prevalence may differ between the 3 groups (see Fig. 2).

For Peer Review

DISCUSSION

This study demonstrates that the prevalence-pattern of a parasite in a metapopulation of hosts can become quite complex and vary in time, space and among sub-groups of hosts. To our knowledge, this is the first empirical study to show such detailed prevalence-dynamics of a macroparasite in a metapopulation of wild avian hosts. Furthermore, our results emphasize the importance of establishing a sampling regime that accounts for seasonal variation in prevalence throughout the year, over several years and spatially among populations in order to achieve a more complete picture of parasite-host dynamics.

The within-year variation in prevalence of *S. trachea* is supported by studies conducted by Barus (1966c). He also found a peak in prevalence of the parasite on poultry farms in Germany in late summer. In concordance with our results Barus (1966b) also found that prevalences dropped to nearly zero during winter time and attributed this pattern to climatic patterns, especially temperature, throughout the year. This link was investigated in another study by Barus (1966a) with experimental observations of egg development time of *S. trachea* from embryo to invasive stage larvae. It was then found that embryos did not develop when the temperature was 16 °C or lower. Development time dropped with increasing temperature and reached an "optimum" of ca. 7 days at 29 °C. This may indicate an important limiting factor for *S. trachea* in our study system which is located on the Arctic Circle. In wintertime, the temperature inside or outside the barns at Helgeland does not exceed the minimal temperature of 16 °C in a normal year (Ringsby *et al.* unpublished results). In summertime, the mean daily temperature recorded by the Norwegian Meteorological Institute's weather stations in the area usually do not exceed 16 °C (Ringsby *et al.*, 2002). Nevertheless, the temperature often exceeds 16 °C in sunlight and under the tin sheet roofs on barns at Helgeland (Ringsby *et al.* unpublished results). Furthermore, there may be several factors other than temperature affecting seasonal parasite prevalence in our population(s), such as for example host density and inter-individual variation between host age-classes and sexes in energy available for defence against the parasite that may change over the breeding season (e.g. Hudson *et al.*, 2002).

The highest ranked model from our first section of analyses also indicated that differences between years was an important contributor to explaining prevalence patterns. Inter-annual variation in prevalence have been found in several other parasite-host systems (Weatherhead and Bennett, 1991; Thompson *et al.*, 1998; Macdonald *et al.*, 1999), and may

For Peer Review

be explained by several factors. For example, climate (Kutz *et al.*, 2005), host population densities (Arneberg, 2001) and vector availability (Weatherhead and Bennett, 1991) may have an effect on the parasite prevalence in a given year. Disentangling what may have caused the temporal patterns observed in this study, should however be a topic for future work.

Our results also indicate that the yearly and within year change in prevalence was not the same on all islands. This may be due to differences in local abiotic conditions among islands (patches), difference in vector availability, or could be caused by genetic differences between islands in either host or parasite. For example, it seems possible that there may be differences between our island populations with respect to genetic variation in the immune system. Accordingly, the island of Aldra, with the highest prevalence of *S. trachea*, has a population history involving a recent population bottleneck and high level of inbreeding (Billing *et al.*, 2012), low effective population size (Engen *et al.* 2007, Baalsrud et al., in review), and low level of "neutral" genetic variation (Jensen *et al.*, 2007, Jensen et al., in review). Although based on very small sample sizes (five individual sparrows from each island population), a recent study suggested however that the level of variation at major histocompatibility complex genes which are important in the vertebrate immune system was similar on Aldra and Hestmannøy (Borg *et al.*, 2011). Other studies have shown that inbreeding may affect parasite prevalence. This was for example found by (Ilmonen *et al.*, 2008) who showed that inbreeding could have a significant negative effect on host (*Mus musculus domesticus*) resistance to *Salmonella*. Alternatively, the differences between islands may be caused by different strains/sub-species of *S. trachea* inhabiting our islands. Spatial differences in strains/sub-species of parasites have been found in other study systems (Bensch and Akesson, 2003; Gaspar da Silva *et al.*, 2007; Wood et al., 2007; Henriques-Gil *et al.*, 2010).There may also be complex interactions between *S. trachea* and other local parasites. We have detected several other parasites inhabiting our study populations (Holand et al., unpublished results), both from our faecal samples (endoparasites: *Isospora spp.*, *Capillaria spp*., *Choanotaenia spp.*) and visual inspection of House Sparrows (ectoparasites: *Hippoboscidae spp.*, *Ornithonyssus spp.*, *Ceratophyllus spp*.). Oocysts of Coccidian (*Isospora spp.*) species were found in 59% of faecal samples while eggs of *Capillaria spp*. and *Choanotaenia spp.* were only found in 0.2% and 0.09% of faecal samples, respectively. Interactions between different parasite species have been demonstrated in other studies (see (Poulin, 2007). However, more detailed studies are needed in order to investigate the relative importance of alternative causes for the different patterns in prevalence between our islands.

For Peer Review

The second section of our analyses revealed that the difference in prevalence between discrete demographic groups explained a substantial part of the total variation in prevalence. Life-stage group (LSG: juvenile, adult male, adult female) seemed to explain more of the variation in prevalence than the simpler age class variable (adult/juvenile). This was partly due to a general difference between the 3 groups, but also due to considerable differences between the groups in both time and space (Fig. 2). Although adult males and females generally had a lower prevalence compared to juveniles, this pattern was opposite in some years on some islands. The apparent difference in prevalence and the relationship between date and prevalence between the demographic groups may be due to unequal exposure to infective stage of the parasite. For instance, Ringsby *et al.* (2009) showed that females in general have a higher feeding rate of nestlings compared to males. If the parasite is transmitted through food items (insects etc.) one may expect the females and nestlings (of which some survive to become juveniles) to show similarities in prevalence (see Zuk and McKean, 1996). On the other hand, differences in prevalence may be caused by differences in immunity. Other studies (Clapham, 1934; Bakke, 1973; Wissler and Halvorsen, 1975) have found higher prevalence of *S. trachea* in juvenile birds. This pattern has been attributed to acquired immunity with age (Atkinson *et al.*, 2008). If this is the case in our populations, one might expect to see a higher prevalence in juveniles compared to adults and that birds rarely get infected more than once. Indeed, out of the 121 birds sampled in more than one year, only 5 birds were shown to be infected in more than one year. This seems to indicate that infection by *S. trachea* is generally a “once in a lifetime” event for our House Sparrows. All these possibilities along with several others (see Zuk and McKean, 1996; McCurdy *et al.*, 1998; Hudson *et al.*, 2002; Lachish *et al.*, 2011) may explain the demographic prevalence patterns observed in our study.

Investigating and understanding parasite prevalence-patterns in space and time is a fundamental step in determining the possible evolutionary and ecological effects parasites may have on host populations. In natural populations, this is however a relatively novel area of research but one that probably will increase in importance as the climate changes and populations are exposed to novel parasites, or effects of parasites are amplified by shortened development time, longer transmission season and reduced generation times expected as a consequence of rising temperatures (see Kutz *et al.* 2005).

For Peer Review

ACKNOWLEDGEMENTS

We would like to thank Lars Erik Andersen, Helle Tessand Baalsrud, Johan Henrik Hårdensson Berntsen, Roger Dahl, Ole Roar Davidsen, Ingerid J. Hagen, Atle Torvik Kristiansen, Thomas Kvalnes, Aline M. Lee, Siri Johansen Monkan, Ane M. Myhre and Henrik Pärn for helping to collect faecal samples. We are also grateful to everyone at Centre of Conservation Biology (CCB) at the Department of Biology, NTNU, for helpful comments and help with statistics in R and lab work. Finally we would like to thank Bjørn Gjerde at the Veterinary Institute in Oslo for taking time out of his busy day in order to teach Håkon Holand the fine art of faecal examination.

FINANCIAL SUPPORT

This study was funded by the Norwegian Research Council and the Norwegian University of Science and Technology. The research was carried out in accordance with permits from the Norwegian Directorate for Nature Management and the Bird Ringing Centre at Stavanger Museum, Norway.

For Peer Review

REFERENCES

Agresti, A. (2002). *Categorical Data Analysis*, Wiley-Interscience.

Aiken, L. and West, S. (1991). *Multiple Regression: Testing and Interpreting Interactions*, Sage Publications, Inc.

Anderson, T. R. (2006). *Biology of the ubiquitous house sparrow: from genes to populations*, Oxford University Press.

Arneberg, P. (2001). An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography*, **24**(3), 352-358. doi: 10.1034/j.1600-0587.2001.240313.x.

Atkinson, C. T., Dusek, R. J., Woods, K. L. and Iko, W. M. (2000). Pathogenicity of avian malaria in experimentally-infected Hawaii Amakihi. *Journal of Wildlife Diseases*, **36**(2), 197-204.

Atkinson, C. T., Thomas, N. J. and Hunter, D. B. (2008). *Parasitic diseases of wild birds*, Wiley-Blackwell.

Bakke, T. A. (1973). STUDIES OF THE HELMINTH FAUNA OF NORWAY PART 27 SYNGAMIASIS IN NORWAY. *Norwegian Journal of Zoology*, **21**(4), 299-303.

Barus, V. (1966a). THE EFFECT OF TEMPERATURE AND AIR HUMIDITY ON THE DEVELOPMENT AND THE RESISTANCE OF EGGS OF THE NEMATODE SYNGAMUS-TRACHEA. *Helminthologia (Bratislava)*, **7**(2), 103-106.

Barus, V. (1966b). THE LONGEVITY OF THE PARASITIC STAGES AND THE DYNAMICS OF EGGS PRODUCTION OF THE NEMATODE SYNGAMUS-TRACHEA IN CHICKEN AND TURKEYS. *Folia Parasitologica (Ceske Budejovice)*, **13**(3), 274-277.

Barus, V. (1966c). SEASONAL DYNAMICS OF THE INVASION EXTENSITY OF THE NEMATODE SYNGAMUS-TRACHEA IN BREEDING TURKEYS MELEAGRIS-GALLOPAVO-F-DOMESTICA. *Helminthologia (Bratislava)*, **7**(1), 29-37.

Barus, V. and Blazek, K. (1965). Revision of exogenous and endogenous phases of the developmental cycle and the pathogenesis of Syngamus (Syngamus) trachea (Montagu, 1811) Chapin, 1925 into the organs of the final host. *Cesk Parasitol*, **12**, 47-70.

Bensch, S. and Akesson, A. (2003). Temporal and spatial variation of hematozoans in Scandinavian willow warblers. *Journal of Parasitology*, **89**(2), 388-391. doi: 10.1645/0022-3395(2003)089[0388:tasvoh]2.0.co;2.

Billing, A. M., Lee, A. M., Skjelseth, S., Borg, Å. A., Hale, M. C., Slate, J. O. N., PÄRn, H., Ringsby, T. H., SÆTher, B.-E. and Jensen, H. (2012). Evidence of inbreeding depression but not inbreeding avoidance in a natural house sparrow population. *Molecular Ecology*, **21**(6), 1487-1499. doi: 10.1111/j.1365-294X.2012.05490.x.

Borg, A. A., Pedersen, S. A., Jensen, H. and Westerdahl, H. (2011). Variation in MHC genotypes in two populations of house sparrow (Passer domesticus) with different population histories. *Ecology and evolution*, **1**(2), 145-159.

Burnham, K. and Anderson, D. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*, Springer.

Clapham, P. A. (1934). Experimental studies on the transmission of gapeworm (Syngamus trachea) by earthworms. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **115**(791), 18-29.

Earn, D. J. D., Rohani, P. and Grenfell, B. T. (1998). Persistence, chaos and synchrony in ecology and epidemiology. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**(1390), 7-10.

For Peer Review

Gaspar da Silva, D., Barton, E., Bunbury, N., Lunness, P., Bell, D. J. and Tyler, K. M. (2007). Molecular identity and heterogeneity of Trichomonad parasites in a closed avian population. *Infection, genetics and evolution : journal of molecular epidemiology and evolutionary genetics in infectious diseases,* **7**(4), 433-440. doi: 10.1016/j.meegid.2007.01.002.

Gjerde, B. (2007). Studypamphlet in Helmintology. (ed. Veterinærhøyskole, N.), Oslo.

Gulland, F. M. D., Albon, S. D., Pemberton, J. M., Moorcroft, P. R. and Cluttonbrock, T. H. (1993). PARASITE-ASSOCIATED POLYMORPHISM IN A CYCLIC UNGULATE POPULATION. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **254**(1339), 7-13.

Gurski, K. C. and Ebbert, M. A. (2003). Host age, but not host location within a stream, is correlated with the prevalence of gut parasites in water striders. *Journal of Parasitology,* **89**(3), 529-534. doi: 10.1645/0022-3395(2003)089[0529:habnhl]2.0.co;2.

Henriques-Gil, N., Haro, M., Izquierdo, F., Fenoy, S. and del Aguila, C. (2010). Phylogenetic Approach to the Variability of the Microsporidian Enterocytozoon bieneusi and Its Implications for Inter- and Intrahost Transmission. *Applied and Environmental Microbiology,* **76**(10), 3333-3342. doi: 10.1128/aem.03026-09.

Hess, G. (1996). Disease in metapopulation models: Implications for conservation. *Ecology,* **77**(5), 1617-1632. doi: 10.2307/2265556.

Hudson, P. J., Dobson, A. P. and Newborn, D. (1998). Prevention of population cycles by parasite removal. *Science,* **282**(5397), 2256-2258.

Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H. and Dobson, A. P. (2002). *The ecology of wildlife diseases,* Oxford University Press.

Ilmonen, P., Penn, D. J., Damjanovich, K., Clarke, J., Lamborn, D., Morrison, L., Ghotbi, L. and Potts, W. K. (2008). Experimental infection magnifies inbreeding depression in house mice. *Journal of Evolutionary Biology,* **21**(3), 834-841. doi: 10.1111/j.1420-9101.2008.01510.x.

Jensen, H., Bremset, E. M., Ringsby, T. H. and Sæther, B. E. (2007). Multilocus heterozygosity and inbreeding depression in an insular house sparrow metapopulation. *Molecular Ecology,* **16**(19), 4066-4078. doi: 10.1111/j.1365-294X.2007.03452.x.

Jensen, H., Steinsland, I., Ringsby, T. H. and Sæther, B. E. (2008). Evolutionary dynamics of a sexual ornament in the house sparrow (passer domesticus): The role of indirect selection within and between sexes. *Evolution,* **62**(6), 1275-1293. doi: 10.1111/j.1558-5646.2008.00395.x.

Jesse, M. and Heesterbeek, H. (2011). Divide and conquer? Persistence of infectious agents in spatial metapopulations of hosts. *Journal of Theoretical Biology,* **275**(1), 12-20. doi: 10.1016/j.jtbi.2011.01.032.

Kutz, S. J., Hoberg, E. P., Polley, L. and Jenkins, E. J. (2005). Global warming is changing the dynamics of Arctic host-parasite systems. *Proceedings of the Royal Society B-Biological Sciences,* **272**(1581), 2571-2576. doi: 10.1098/rspb.2005.3285.

Lachish, S., Knowles, S. C. L., Alves, R., Wood, M. J. and Sheldon, B. C. (2011). Infection dynamics of endemic malaria in a wild bird population: parasite species-dependent drivers of spatial and temporal variation in transmission rates. *Journal of Animal Ecology,* **80**(6), 1207-1216. doi: 10.1111/j.1365-2656.2011.01893.x.

Macdonald, D. W., Anwar, M., Newman, C., Woodroffe, R. and Johnson, P. J. (1999). Inter-annual differences in the age-related prevalences of Babesia and Trypanosoma parasites of European badgers (Meles meles). *Journal of Zoology,* **247**, 65-70. doi: 10.1111/j.1469-7998.1999.tb00193.x.

For Peer Review

McCurdy, D. G., Shutler, D., Mullie, A. and Forbes, M. R. (1998). Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. *Oikos*, **82**(2), 303-312. doi: 10.2307/3546970.

Pärn, H., Jensen, H., Ringsby, T. H. and Sæther, B. E. (2009). Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. *Journal of Animal Ecology*, **78**(6), 1216-1225. doi: 10.1111/j.1365-2656.2009.01597.x.

Pärn, H., Ringsby, T. H., Jensen, H. and Sæther, B. E. (2012). Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation. *Proceedings of the Royal Society B-Biological Sciences*, **279**(1726), 144-152. doi: 10.1098/rspb.2011.0673.

Poulin, R. (2007). *Evolutionary Ecology of Parasites*, Princeton University Press.

Ringsby, T. H., Berge, T., Sæther, B. E. and Jensen, H. (2009). Reproductive success and individual variation in feeding frequency of House Sparrows (Passer domesticus). *Journal of Ornithology*, **150**(2), 469-481. doi: 10.1007/s10336-008-0365-z.

Ringsby, T. H., Sæther, B. E., Tufto, J., Jensen, H. and Solberg, E. J. (2002). Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology*, **83**(2), 561-569.

Saunders, D. A., Hobbs, R. J. and Margules, C. R. (1991). BIOLOGICAL CONSEQUENCES OF ECOSYSTEM FRAGMENTATION - A REVIEW. *Conservation Biology*, **5**(1), 18-32. doi: 10.1111/j.1523-1739.1991.tb00384.x.

Sæther, B. E., Ringsby, T. H., Bakke, O. and Solberg, E. J. (1999). Spatial and temporal variation in demography of a house sparrow metapopulation. *Journal of Animal Ecology*, **68**(3), 628-637.

Thompson, P. M., Corpe, H. M. and Reid, R. J. (1998). Prevalence and intensity of the ectoparasite Echinophthirius horridus on harbour seals (Phoca vitulina): effects of host age and inter-annual variability in host food availability. *Parasitology*, **117**, 393-403. doi: 10.1017/s0031182098003072.

Vogeli, M., Lemus, J. A., Serrano, D., Blanco, G. and Tella, J. L. (2011). An island paradigm on the mainland: host population fragmentation impairs the community of avian pathogens. *Proceedings of the Royal Society B-Biological Sciences*, **278**(1718), 2668-2676. doi: 10.1098/rspb.2010.1227.

Weatherhead, P. J. and Bennett, G. F. (1991). ECOLOGY OF RED-WINGED BLACKBIRD PARASITISM BY HEMATOZOA. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **69**(9), 2352-2359. doi: 10.1139/z91-331.

Wissler, K. and Halvorsen, O. (1975). THE OCCURRENCE OF GAPEWORM SYNGAMUS-TRACHEA IN WILLOW GROUSE. *Journal of Wildlife Diseases*, **11**(2), 245-247.

Wood, M. J., Cosgrove, C. L., Wilkin, T. A., Knowles, S. C. L., Day, K. P. and Sheldon, B. C. (2007). Within-population variation in prevalence and lineage distribution of avian malaria in blue tits, Cyanistes caeruleus. *Molecular Ecology*, **16**(15), 3263-3273. doi: 10.1111/j.1365-294X.2007.03362.x.

Yamaguti, S. (1961). *Systema helminthum. Vol. Ill, pts. I-II. The Nematodes of Vertebrates*, (Interscience Publishers).

Zuk, M. and McKean, K. A. (1996). Sex differences in parasite infections: Patterns and processes. *International Journal for Parasitology*, **26**(10), 1009-1023. doi: 10.1016/s0020-7519(96)00086-0.

For Peer Review

Appendix 1

Table listing the estimates and standard errors from the top model in an AICc comparison of generalized linear mixed models explaining prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast of Helgeland in northern Norway. All models included individual identity as a random factor. Data was collected on 4 islands during the breeding season (1.May – 17.August) in the years 2007-2010. SDN is a continuous variable indicating which day during the breeding season a bird was sampled. Interaction terms between two variables are denoted A x B. Intercept contains the estimates of the year 2007 and the island Gjerøy.

Coefficients	Estimates	Standard errors
Intercept	-9.8200	3.0500
SDN	0.1160	0.1210
SDN^2	-0.0019	0.0020
YEAR 2008	-3.0500	2.9800
YEAR 2009	-9.7100	4.8600
YEAR 2010	-15.0000	4.8100
ISLAND Hestmannøy	-0.0676	2.5700
ISLAND Indre Kvarøy	1.4600	4.6300
ISLAND Aldra	16.2000	5.4200
SDN × YEAR 2008	0.0727	0.0632
SDN × YEAR 2009	-0.0163	0.0765
SDN × YEAR 2010	0.2710	0.0864
SDN × ISLAND Hestmannøy	0.0243	0.1090
SDN × ISLAND Indre Kvarøy	-0.2630	0.2190
SDN × ISLAND Aldra	-0.1240	0.1100
SDN^2 × ISLAND Hestmannøy	-0.0006	0.0021
SDN^2 × ISLAND Indre Kvarøy	0.0050	0.0039
SDN^2 × ISLAND Aldra	-0.0045	0.0025
YEAR 2008 × ISLAND Hestmannøy	0.8450	2.1600
YEAR 2009 × ISLAND Hestmannøy	9.4500	4.2500
YEAR 2010 × ISLAND Hestmannøy	1.9500	3.0700
YEAR 2008 × ISLAND Indre Kvarøy	-19.4000	250.0000
YEAR 2009 × ISLAND Indre Kvarøy	10.1000	5.2900
YEAR 2010 × ISLAND Indre Kvarøy	1.5000	3.5400
YEAR 2008 × ISLAND Aldra	-10.4000	4.9300
YEAR 2009 × ISLAND Aldra	-2.8900	6.0400
YEAR 2010 × ISLAND Aldra	13.6000	5.4000

For Peer Review

Appendix 2

Table listing the estimates and standard errors from the top model in an AICc comparison of generalized linear mixed models explaining prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast of Helgeland in northern Norway. All models included individual identity as a random factor. Data was collected on 4 islands during the breeding season (1.May – 17.August) in the years 2007-2010. SDN is a continuous variable indicating which day during the breeding season a bird was sampled. LSG is a categorical variable denoting the 3 main demographic groups in house sparrow populations: adult males, adult females and juveniles. Interaction terms between two variables are denoted A x B. Note that models with interactions also include the main effects of A and B. Intercept contains the estimates of the year 2007, the island Gjerøy and adult females.

Coefficients	Estimates	Standard errors
Intercept	-9.4100	5.6900
SDN	0.0737	0.1220
SDN^2	-0.0030	0.0025
YEAR 2008	-12.2000	5.1900
YEAR 2009	-19.8000	6.4800
YEAR 2010	-22.0000	6.7100
ISLAND Hestmannøy	-0.9170	5.1600
ISLAND Indre Kvarøy	19.5000	7.0600
ISLAND Aldra	40.9000	9.2000
LSG Juvenile	1.0100	4.5800
LSG Adult Male	-24.3000	8.5800
SDN × YEAR 2008	0.1640	0.1040
SDN × YEAR 2009	-0.0235	0.1060
SDN × YEAR 2010	0.3060	0.1310
SDN × ISLAND Hestmannøy	0.1100	0.0897
SDN × ISLAND Indre Kvarøy	-0.2440	0.2270
SDN × ISLAND Aldra	-0.0775	0.0887
SDN^2 × ISLAND Hestmannøy	-0.0005	0.0022
SDN^2 × ISLAND Indre Kvarøy	0.0060	0.0043
SDN^2 × ISLAND Aldra	-0.0047	0.0028
YEAR 2008 × ISLAND Hestmannøy	1.5500	3.2600
YEAR 2009 × ISLAND Hestmannøy	12.5000	5.1500
YEAR 2010 × ISLAND Hestmannøy	1.2800	4.1700
YEAR 2008 × ISLAND Indre Kvarøy	-35.9000	625.0000
YEAR 2009 × ISLAND Indre Kvarøy	-3.1500	9.9600
YEAR 2010 × ISLAND Indre Kvarøy	-9.5700	7.2300
YEAR 2008 × ISLAND Aldra	-27.0000	7.8800
YEAR 2009 × ISLAND Aldra	-22.7000	8.7100
YEAR 2010 × ISLAND Aldra	-2.0700	7.8900
SDN^2 × LSG Juvenile	0.0001	0.0015
SDN^2 × LSG Adult Male	0.0030	0.0016
YEAR 2008 × LSG Juvenile	6.2900	3.5800
YEAR 2009 × LSG Juvenile	8.9500	3.8200
YEAR 2010 × LSG Juvenile	8.6200	3.8500

For Peer Review

YEAR 2008 × LSG Adult Male	26.4000	5.5100
YEAR 2009 × LSG Adult Male	31.7000	6.5900
YEAR 2010 × LSG Adult Male	24.2000	5.6200
ISLAND Hestmannøy × LSG Juvenile	-2.8200	3.7700
ISLAND Indre Kvarøy × LSG Juvenile	-19.1000	6.2500
ISLAND Aldra × LSG Juvenile	-31.0000	8.1100
ISLAND Hestmannøy × LSG Adult Male	-4.3600	5.9500
ISLAND Indre Kvarøy × LSG Adult Male	-8.0500	7.4500
ISLAND Aldra × LSG Adult Male	-4.1700	6.4600

For Peer Review

Tables

Table 1: Top 10 (of 44) models in an AICc comparison of generalized linear mixed models explaining prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast of Helgeland in northern Norway. All models included individual identity as a random factor. Data was collected on 4 islands during the breeding season (1.May – 17.August) in the years 2007-2010. SDN is a continuous variable indicating which day during the breeding season a bird was sampled. Interaction terms between two variables are denoted A x B. Note that models with interactions also include the main effects of A and B.

Model	DF	ΔAICc	AICc weight
SDN × YEAR + SDN × ISLAND + SDN^2 × ISLAND + ISLAND × YEAR	28	0.00	0.8821
SDN × YEAR + SDN^2 × ISLAND + ISLAND × YEAR	25	4.27	0.1043
SDN^2 × YEAR + SDN × ISLAND + ISLAND × YEAR	25	9.84	0.0064
SDN^2 × YEAR + SDN × ISLAND + SDN^2 × ISLAND + ISLAND × YEAR	28	11.01	0.0036
SDN × YEAR + SDN × ISLAND + ISLAND × YEAR	24	11.25	0.0032
SDN × ISLAND + SDN^2 × ISLAND + ISLAND × YEAR	25	18.10	0.0001
SDN + SDN^2 × ISLAND + ISLAND × YEAR	22	18.41	< 0.0001
SDN × YEAR + ISLAND × YEAR	21	19.46	< 0.0001
SDN^2 + SDN × ISLAND + ISLAND × YEAR	22	20.22	< 0.0001
SDN^2 + SDN × YEAR	10	21.79	< 0.0001

Table 2: Top 10 (of 31) models in an AICc comparison of generalized linear mixed models explaining prevalence of the parasite *Syngamus trachea* in a metapopulation of house sparrows on the coast of Helgeland in northern Norway. All models included individual identity as a random factor. Data was collected on 4 islands during the breeding season (1.May – 17.August) in the years 2007-2010. SDN is a continuous variable indicating which day during the breeding season a bird was sampled. Ageclass is a categorical variable dividing house sparrows into juveniles and adults. LSG is a categorical variable denoting the 3 main demographic groups in house sparrow populations: adult males, adult females and juveniles. All models also contain the terms from the best model in a previous model comparison (SDN × YEAR + SDN × ISLAND + SDN^2 × ISLAND + ISLAND × YEAR, see Table 1). Interaction terms between two variables are denoted A x B. Note that models with interactions also include the main effects of A and B.

For Peer Review

Model	DF	ΔAICc	AICc weight
LSG × ISLAND + LSG × YEAR + LSG × SDN^2	44	0.00	0.5694
LSG × ISLAND + LSG × YEAR	42	0.96	0.3528
LSG × ISLAND + LSG × YEAR + LSG × SDN	44	5.14	0.0435
AGECLASS × ISLAND	32	7.85	0.0112
AGECLASS × ISLAND + AGECLASS × SDN^2	33	8.71	0.0073
AGECLASS × ISLAND + AGECLASS × SDN	33	8.93	0.0065
LSG × SDN^2 + LSG × SDN	34	10.52	0.0030
AGECLASS × ISLAND + AGECLASS × SDN + AGECLASS × SDN^2	34	10.84	0.0025
AGECLASS × ISLAND + AGECLASS × YEAR	35	13.08	0.0008
LSG × ISLAND	36	14.09	0.0005

For Peer Review

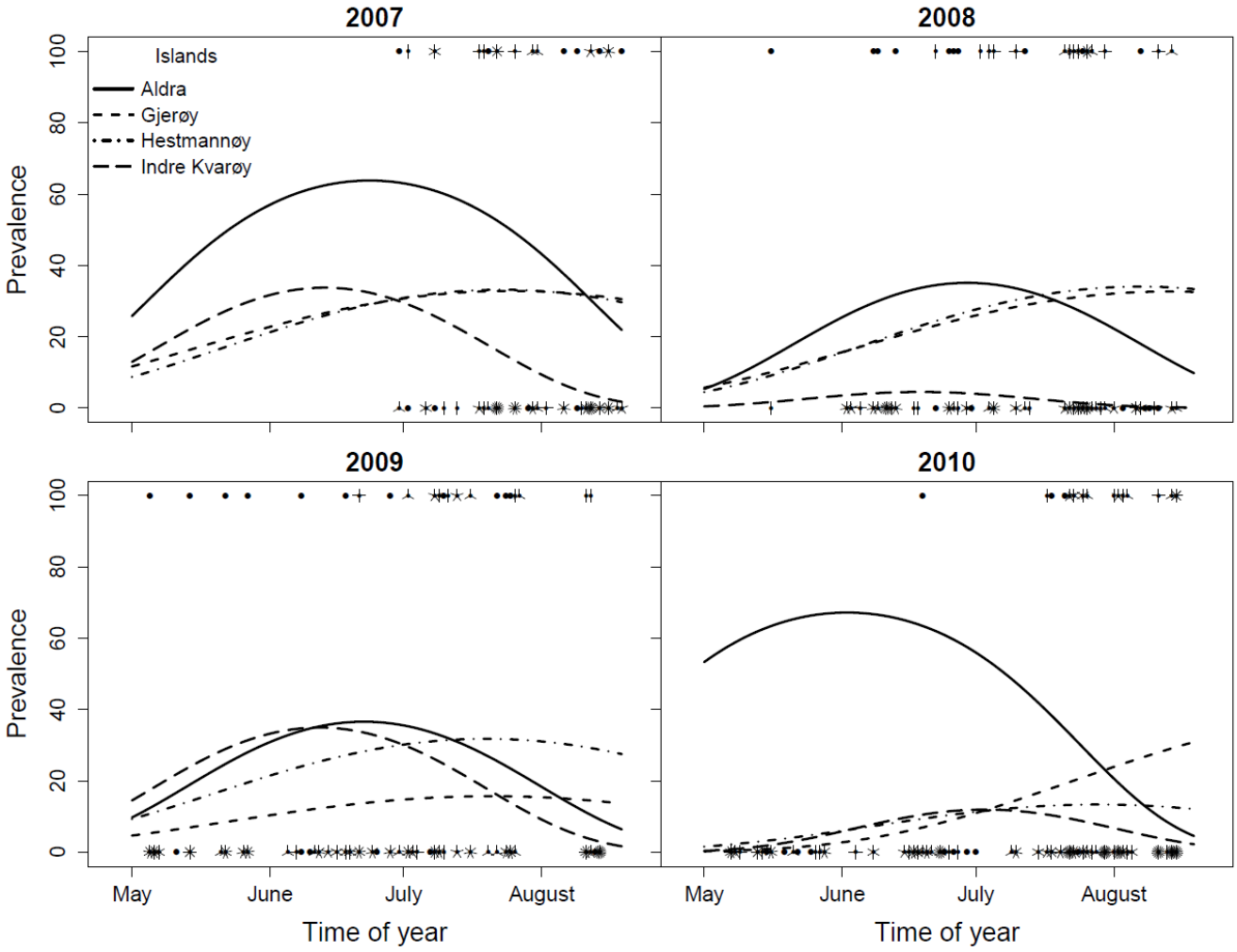
Figure legends

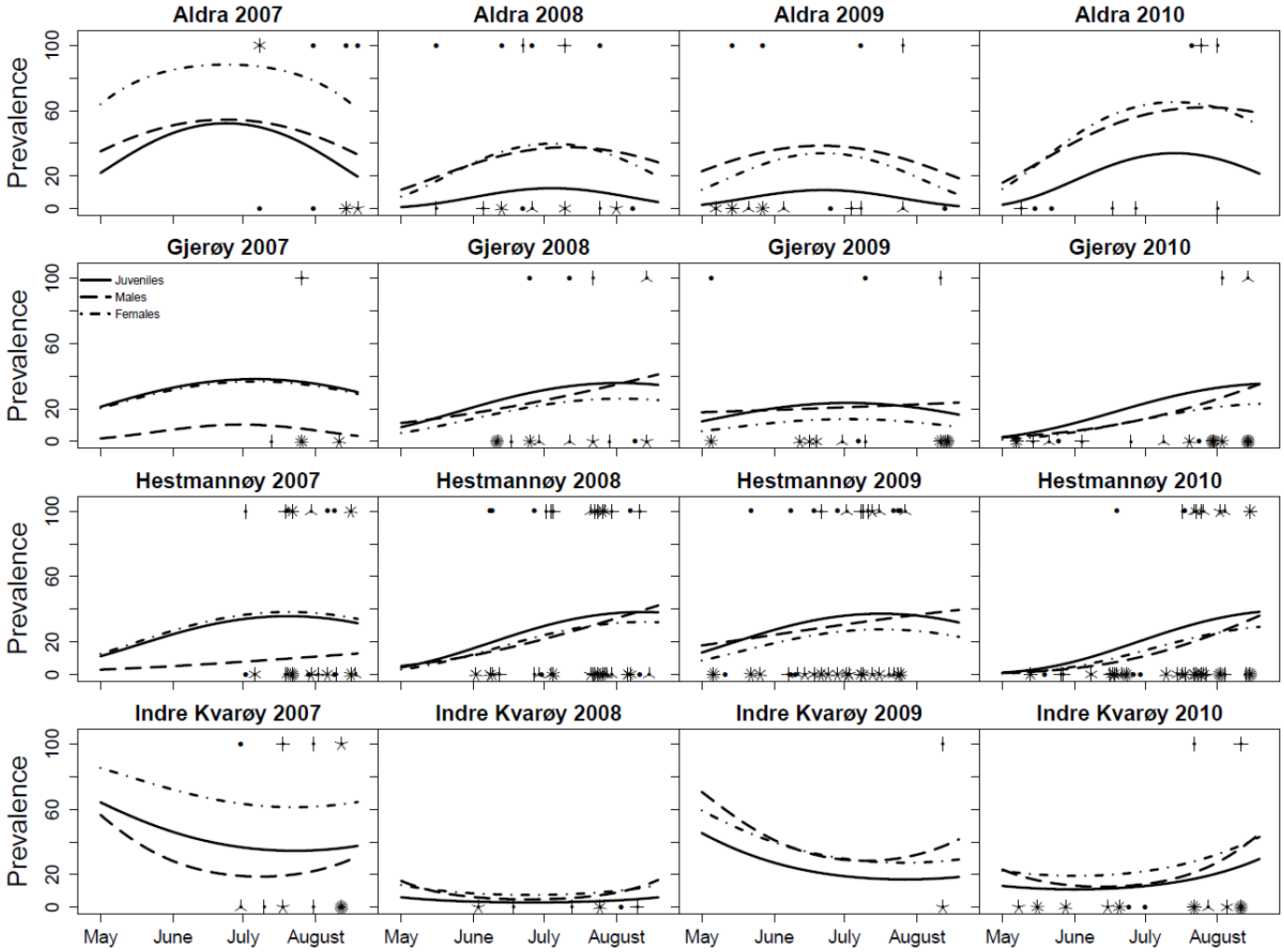
Fig. 1: Graphical presentation of predictions from the best generalized linear mixed model describing prevalence of the parasite *Syngamus trachea* in an insular metapopulation of House Sparrows on the coast of Helgeland in northern Norway. The response variable in the model was the binary occurrence (1) or absence (0) of eggs in faeces of House Sparrows. Individual identity was used as a random factor. Data was obtained from faecal samples from 4 islands during the breeding seasons of the years 2007 – 2010. The predicted relationships from the model between season and prevalence for the four islands are plotted as lines. Sample sizes are shown as "sunflower" points denoting number of negative (individual prevalence = 0%) and positive (individual prevalence = 100%) samples, respectively.

Fig. 2: Graphical presentation of predictions from the best generalized linear mixed model describing prevalence of the parasite *Syngamus trachea* in an insular metapopulation of House Sparrows on the coast of Helgeland in northern Norway. The response variable in the model was the binary occurrence (1) or absence (0) of eggs in faeces of House Sparrows of different life-stage groups (juvenile, adult female or adult male). Individual identity was used as a random factor. Data was obtained from faecal samples from 4 islands during the breeding seasons of the years 2007 – 2010. Sample sizes are shown as "sunflower" points denoting number of negative (individual prevalence = 0%) and positive (individual prevalence = 100%) samples, respectively.

For Peer Review

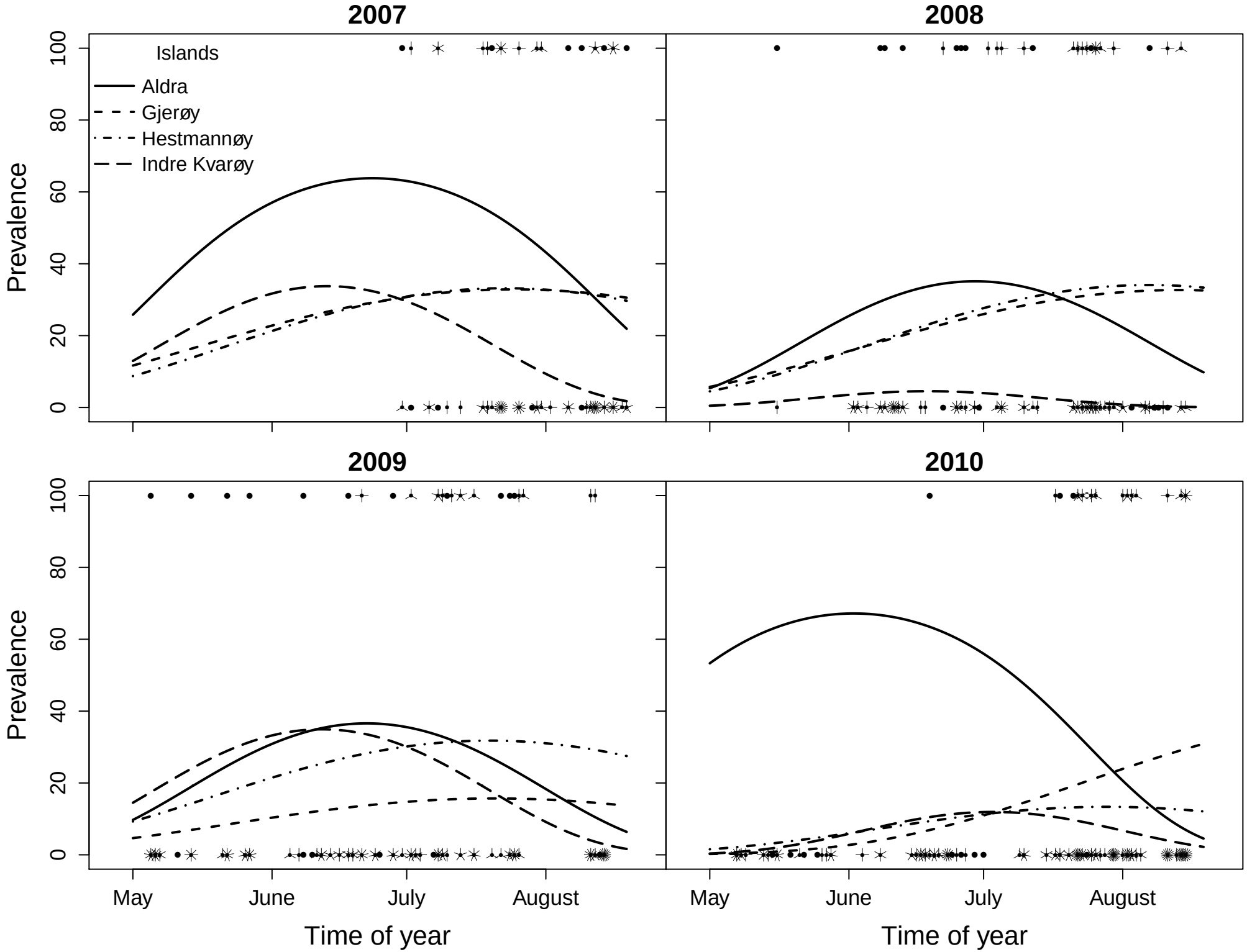
Figures

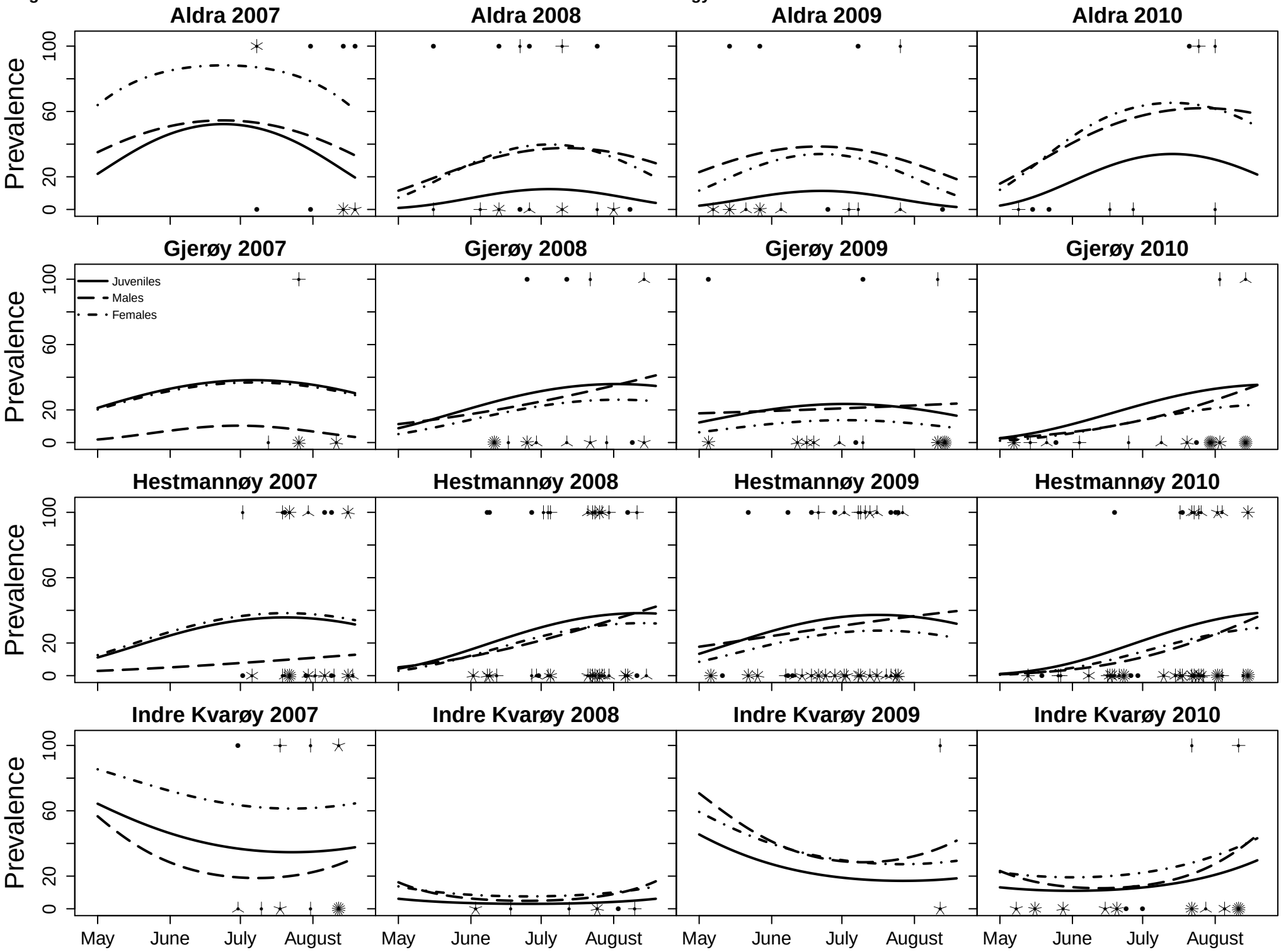

2007
2008
2009
2010
Islands
Aldra
Gjerøy
Hestmannøy
Indre Kvarøy
Prevalence
0
20
40
60
80
100
May
June
July
August
Time of year


Aldra 2007
Aldra 2008
Aldra 2009
Aldra 2010
Gjerøy 2007
Gjerøy 2008
Gjerøy 2009
Gjerøy 2010
Hestmannøy 2007
Hestmannøy 2008
Hestmannøy 2009
Hestmannøy 2010
Indre Kvarøy 2007
Indre Kvarøy 2008
Indre Kvarøy 2009
Indre Kvarøy 2010
Prevalence
0
20
60
100
Juveniles
Males
Females
May
June
July
August

775

eview


2007
2008
2009
2010
Islands
Aldra
Gjerøy
Hestmannøy
Indre Kvarøy
Prevalence
0
20
40
60
80
100
May
June
July
August
Time of year


Aldra 2007
Aldra 2008
Aldra 2009
Aldra 2010
Gjerøy 2007
Gjerøy 2008
Gjerøy 2009
Gjerøy 2010
Hestmannøy 2007
Hestmannøy 2008
Hestmannøy 2009
Hestmannøy 2010
Indre Kvarøy 2007
Indre Kvarøy 2008
Indre Kvarøy 2009
Indre Kvarøy 2010
Prevalence
0
20
60
100
Juveniles
Males
Females
May
June
July
August