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Ectoparasite (*Ceratophyllus vagabundus vagabundus)* infestations reduce hatching success in precocial birds (*Branta leucopsis*) nesting in the High Arctic

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"Great fleas have little fleas upon their backs to bite 'em,
And little fleas have lesser fleas, and so ad infinitum."

-Augustus De Morgan, *A Budget of Paradoxes*

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Ross T. Wetherbee

Abstract

Arctic terrestrial ecosystems are ideal systems to study host-parasite interactions because they are sensitive and have fewer confounding interactions than lower latitudes. Since the Arctic is experiencing rapid climate change, research there can provide models to better understand and predict future changes in other systems. The Barnacle goose (*Branta leucopsis*) and its ectoparasite the flea (*Ceratophyllus vagabundus vagabundus*) is an ideal Arctic host-parasite system to study because Barnacle geese have important roles in Arctic ecosystems as selective grazers and prey items and have been intensively studied for decades. Also, recent studies suggest that Arctic avian flea infestations may be increasing, possibly due to climate change. However, few studies have considered the effect of fleas on Arctic nesting birds and little is known of Arctic avian flea ecology, most importantly whether they overwinter in the High Arctic or are reintroduced each summer by migrating birds. Furthermore, sampling methods for avian fleas are time-consuming and semi-invasive to their hosts. Therefore, the project had four aims: (i) contribute to the knowledge of Arctic flea ecology by looking for evidence of overwintering, (ii) use an experimental study to assess the impact of flea infestations on the hatching success of Barnacle goose eggs, (iii) assess the simple and disturbance-free method of estimating fleas with photographs of blood spots on goose eggs, (iv) and test the results of both the experimental study as well as the application of blood spots as a proxy measure for flea infestations through a larger observational study. It was found that fleas were likely overwintering in empty nest bowls and some evidence indicated that they might be capable of a two-year life cycle in the High Arctic. The findings from the experimental study indicated that heavy flea infestations had a negative impact on the hatching success of Barnacle goose eggs. It was also determined that blood spots were a good proxy measure of flea infestations, but become less accurate through incubation due to wear from incubating birds. Finally, the observational study supported the findings of the experimental study and demonstrated the power and simplicity of using blood spots as a proxy measure for flea infestations. Based on these findings, it is suggested that researchers interested in either reproductive success or incubation behavior of Barnacle geese should include a measure of flea infestations in their studies and using blood spots as a proxy measure is a simple and disturbance-free method of doing this.

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1. Introduction

It is well documented that predation, competition and environmental conditions regulate species occurrences and dynamics (Manuel & Molles 2008). However, the effect of parasites in ecosystems has received considerably less attention. This lack of research on parasites is further exacerbated by the fact that the main focus of most ecological research on parasites has been on the impacts of newly emerged parasites on naïve host populations, with less attention on the nearly ubiquitous effects of endemic parasites (Pedersen & Fenton 2015).

The host-parasite system has limited research in the field of ecology, partly due to its complexity (Pedersen & Fenton 2015). The lack of research on Arctic host-parasite interactions is a missed opportunity because terrestrial Arctic ecosystems have relatively simple tropic interactions, and therefore are ideal systems to study these complex interactions (Davidson *et al.* 2011; Strathdee & Bale 1998; Hodkinson & Coulson 2004). Furthermore, research suggests that climate change is currently altering parasite-host interactions in the Arctic (Davidson *et al.* 2011; Dobson *et al.* 2015). Research in this region is critical to identify changes that are occurring, and could provide models to better understand and predict climate change induced impacts on other host-parasite systems (Bradley *et al.* 2005; Davidson *et al.* 2011; Epstein 2002).

As a group, birds have been studied extensively (Clayton *et al.* 2010). This is also true in the Arctic where there are detailed and long running data sets regarding Arctic-breeding birds (Loonen & Tombre 1998; Norwegian Polar Institute MOSJ). The study of Arctic avian parasites is a logical starting point for understanding host-parasite dynamics in the Arctic, because there is a large body of work to draw from regarding avian ecology and population dynamics. Furthermore, there is a growing body of work on avian ectoparasites in the Arctic (Harriman *et al.* 2008; Harriman & Alisauskas 2010; Harriman *et al.* 2011; Gwiazdowicz *et al.* 2012; Pilskog *et al.* 2014).

The flea is an important avian ectoparasite (Lopez-Rull & Garcia 2015; Wall & Shesarer 2001). Fleas in high densities are capable of posing heavy energetic cost on their hosts through significant blood loss, and even in low densities fleas can cause irritation to their hosts, as a result of their hemorrhagic saliva (Wall & Shesarer 2001). Fleas also

have been shown to reduce reproductive success in birds (Fitze *et al.* 2004; Harriman & Alisauskas 2010; Loye & Carroll 1998; Brown *et al.* 1995; Richner *et al.* 1993; Oppliger at al 1994).

The Barnacle goose (*Branta leucopsis*) and its ectoparasite the flea, *Ceratophyllus vagabundus vagabundus*, Boheman (1866) is an ideal Arctic host-parasite system to study. Barnacle geese have few other parasites as opposed to Common Eider ducks (*Somateria mollissima*) (Hanssen *et al.* 2003). Also, they are easily accessed since they nest in colonies on small islands or near the coast as opposed to Pink-footed geese (*Anser brachyrhynchus*), and have a well known ecology as opposed to Brent geese (*Branta bernical)*(Strøm 2006). Since many of the Barnacle geese that nest in Kongsfjorden, Svalbard graze in the nearby research village of Ny-Ålesund just after hatching, it is easy to measure breeding success. Furthermore, there is a detailed and long running data set connected to the colonies nesting in Kongsfjorden, Svalbard (Black et al. 2014; Loonen 2005; Loonen *et al.* 1999; Loonen *et al*. 1998; Loonen *et al*. 1997).

Barnacle geese also have an important role in the functioning of Arctic ecosystems. They affect plant communities through intensive and selective grazing (Strøm 2006; Black *et al.* 2014). They also serve as important prey items for Arctic nesting predatory birds such as the Glaucous gull (*Larus hyperboreus*) and skuas (*Stercorarius sp.*), as well as the Arctic fox (*Vulpes lagopus*) (Loonen 2005; Strøm 2006). Recently, studies have shown that Arctic nesting geese are becoming important food items for some Polar bears (*Ursus maritimus*) that are unable to hunt seals due to reduced sea ice (Rockwell & Gormezano 2009; Rockwell *et al.* 2011).

Fleas inhabiting bird nests in Svalbard have been noted as early as 1930 (Thor 1930). In the Canadian Arctic, studies have shown an increase of flea infestations in goose colonies since the early 2000s (Harriman *et al.* 2011; Harriman & Alisauskas 2010; Harriman *et al.* 2008). This may be a circumpolar event. In Svalbard, Pilskog *et al.* (2014) found fleas present in all sea bird and waterfowl nests sampled. Studies in the Arctic have found that fleas are highly aggregated and can have large populations in some nests (Coulson 2013; Pilskog *et al.* 2014; Cypric & Krumpal 1991; Mehl 1992).

Although occurrences of avian fleas are well documented in the Arctic, it is unknown if they are overwintering in Svalbard or are transported yearly by migrating birds

(Pilskog *et al.* 2014). It is important to have knowledge of the dynamics of flea populations because it has implications for understanding how they will affect goose behavior, such as nest site choice, as well as predicting their influences on the goose colonies and the response of this host-parasite system to climate change.

In many ways this is an ideal Arctic host-parasite system to study, but there are challenges to studying avian fleas. One of the greatest challenges for studying parasites in general is obtaining accurate measures of the parasites without influencing the hosts. Current methodology for estimating flea populations in nests involves the semi-invasive, time-consuming and resource-demanding process of collecting nest material and extracting the fleas (Pilskog *et al.* 2014). It is necessary to take only small samples so that insulation of the nests is not compromised, and repeat sampling is problematic because birds add little down to the nests through incubation. Furthermore, the logistical challenges of working in the field combined with the mobility of adult fleas makes this a less than ideal method for establishing accurate measures of flea abundances. It has been suggested that a simple and easy alternative could be to estimate fleas by using the percent of eggs covered by blood (blood spots) as a proxy measure (Harriman *et al.* 2008).

The occurrence of blood spots on bird eggs has been attributed to flea infestations for years. Askew (1971) speculated that blood spots appear on eggs after adult fleas feed excessively and defecate partially digested blood to feed their larvae. Harriman *et al.* (2008) concluded, "The proportion of eggs covered by blood was a good index of flea abundance in the nest." It may therefore be possible to estimate flea abundances by considering blood spots. If this method were to be confirmed it would remove a major obstacle for future research.

In light of this, the project had four aims: (i) better understand flea dynamics by looking for evidence of overwintering *C. v. vagabundus* in Svalbard, (ii) study this host-parasite system with the use of an experiment to asses the impact of flea infestations on the hatching success of Barnacle goose eggs, (iii) assess the novel and relatively disturbance free method of estimating flea abundances with photographs of blood spots on goose eggs, (iv) and test the results of both the experimental study and the application of blood spots as a proxy measure for flea infestations through a larger observational

study. The predictions of this study are: (i) *C. v. vagabundus* is overwintering in Svalbard in the soil of the abandoned nest bowls, (ii) heavy flea infestations will cause incubating birds to spend less time on the nest, reducing hatching success, (iii) percent of eggs covered in blood spots will be a significant predictor of number of fleas in the nest, (iv) and blood spots will be a negative predictor of goose egg hatching success in the larger observational study.

2. Material and Methods

2.1 Study site

Svalbard is located ~700 km north of mainland Europe, between 74° and 81°N, and 10° and 35°E. It has a land area of ~63,000 km^2, 60% of this is glaciated or permanently snow covered (Figure 2.1). Norway has had sovereignty (with some restrictions) over Svalbard since the Svalbard Treaty went into effect in 1925. However, the Norwegian state practices nondiscrimination in the case of scientific activities in Svalbard (Coulson 2013).

Kongsfjorden is located on the west coast of Spitsbergen, the largest island in Svalbard (Figure 2.2). The research town of Ny-Ålesund is located within Kongsfjorden. The summers in Kongsfjorden are short with average temperatures between 0° and 5°C from June to September, and the winters are long with temperatures averaging between -10° and -15°C. Kongsfjorden has low precipitation with the highest amount in the fall, and a short period free of snow lasting from June to September (Norwegian Meteorology Institute 2014).

Figure 2.1: Svalbard (outlined in red) located ~700 km north of mainland Europe, has an area of 63,000 km^2 of which 60% is permanently snow or ice covered (Google Maps).

Kongsfjorden contains approximately 15 islands of notable size, many of which have bird colonies on them in the summer (Figure 2.2). Storholmen (30 ha) has the largest Barnacle goose colony within Kongsfjorden, and was made a bird sanctuary in 1973 (Tombre *et al.* 1998; Strøm 2006; Sysselmannen of Svalbard 2010). The Storholmen Barnacle goose colony was established in the 1980s and has subsequently increased to over 100 nesting pairs in the summer of 2014 (Tombre *et al.* 1998; Loonen *unpublished data*). The 2014 bird colony primarily consisted of Barnacle geese and Common Eider ducks as well as Arctic Terns (*Sterna paradisaea*). The predatory birds nesting on Storholmen during this time period were Glaucous gulls, Great skuas (*S. skua*) and Arctic skuas (*S. parasiticus*). Additionally, the island had between two and three reindeer (*Rangifer tarandus platyrhynchus*) throughout the summer. In July the colony was visited by a polar bear, which predated some of the Barnacle goose and Common Eider duck nests.

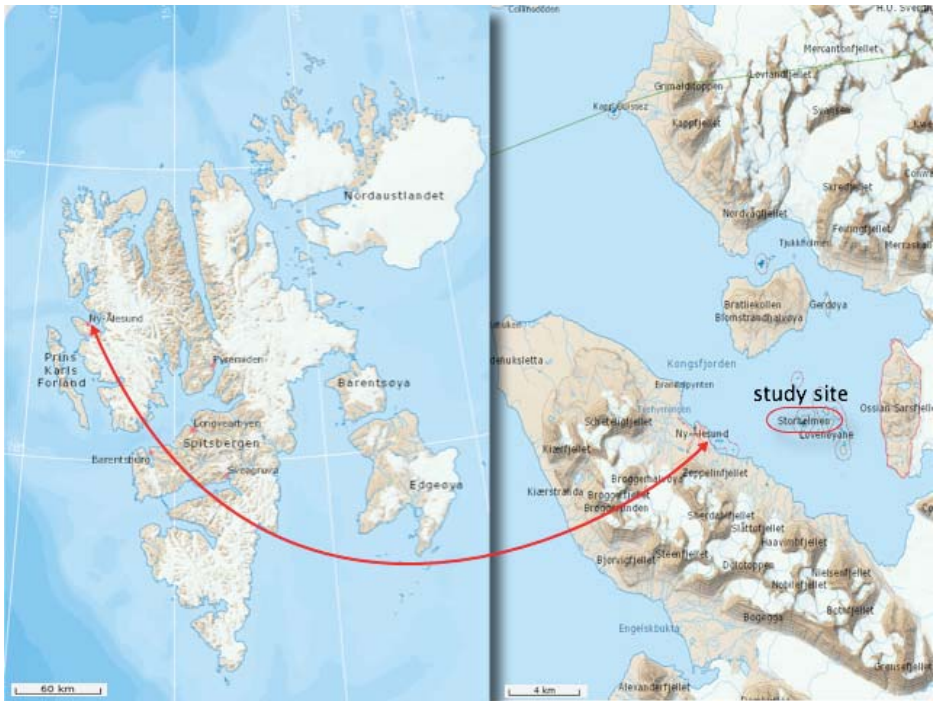

Figure 2.2: Svalbard (located between 74° and 81° north and 10° and 35° east) with map of Kongsfjorden and the study site on Storholmen circled in red (Norwegian Polar Institute, 2015)

2.2 Study species

2.2.1 The Barnacle goose

Barnacle geese are generally considered Arctic breeders, although some are now breeding in more southern locations (Strøm 2006; Van der Jeugd *et al.* 2009). There are three populations: one in east Greenland, one in western Siberia, and one in Svalbard (Boyd 1961; Owen & Norderhaug 1977; Strøm 2006). Their numbers in Svalbard have significantly increased since a population bottleneck in the 1940s to approximately 30,000 (Owen & Norderhaug 1977; Strøm 2006; Tombre *et al.* 1998; Black *et al.* 2014). The Svalbard population overwinters in Solway Firth in southern Scotland (Strøm 2006; Black *et al*. 2014).

Barnacle geese become sexually mature at 3 years and can live up to 25 years (Strøm 2006). The geese nest in both solitary pairs and in dense colonies that are often located on small islands in fjords or places with a vantage point (Owen & Norderhaug 1977; Strøm 2006; Tombre *et al.* 1998). This is assumed to reduce predation by arctic fox, while giving the incubating birds access to food (Strørm 2006; Tombre *et al.* 1998). Nests are built by females, and are reused from one year to the next. Nests are a small depression in the soil lined with down from the parents. These depressions often build up over the years as they are reused and become vegetated (Strøm 2006).

Barnacle geese have some annual variation regarding when they begin incubation. In typical years it begins in late May or early June, but it may take place later depending on snow conditions (Owen & Norderhaug 1977; Tombre *et al.* 1998; Black *et al.* 2014). Once incubation begins it lasts 24 to 25 days (Strøm 2006). The geese typically lay between 2 and 5 eggs (Owen & Norderhaug 1977; Black *et al.* 2014). Only the female incubates, but the male remains within close proximity during this period to protect the nests from predation (Strøm 2006). Barnacle goose hatchlings are precocial (hatch with feathers and site and can soon forage independently) and leave the nest immediately after hatching (Starck & Ricklefs 1998; Strøm 2006).

2.2.2 The flea, C. v. vagabundus

C. v. vagabundus is in the order of Siphonaptera and the subfamily Ceratophylliae (Brinck-Lindroth & Smit 2007, see Apendix Figure 6.2C for photo). Flea species from

the subfamily Ceratophylliae parasitize birds and are primarily found in the Arctic and sub-Arctic (Brinck-Lindroth & Smit 2007; Wall & Shesarer 2001). Adult fleas are well adapted for ectoparasitic life; they are wingless and have laterally flattened, hairy bodies (Brinck-Lindroth & Smit 2007; Wall & Shesarer 2001). *C. v. vagabundus* adults are 2.8 to 3.4 mm and are shiny brown in color (Brinck-Lindroth & Smit 2007). Diagnostic traits of adults include: 24 or more spines on the pronotum (all bird fleas), spines of pronotal ctenidium are much shorter than pronotum, strait posterior margin of sternum, spermatheca as in figure 113, genital ducts as in figure 112, as well as spiracular fossae of terga that is large with an elongated extension (Appendix: Figure 6.2E, Brinck-Lindroth & Smit 2007). Females of *C. v. vagabundus* are indistinguishable from females of *C. v. insularis*, but males are separated by differences in the posterior part of the distal arm (Appendix: Figure 6.2E, Brinck-Lindroth & Smit 2007).

Flea larvae are similar in appearance: elongated with 13 body segments, long setae, and a distinct head capsule, which is eyeless and has chewing mouth parts (Appendix: Figure 6.2D, Brinck-Lindroth & Smit 2007; Harriman *et al.* 2011; Wall & Shesarer 2001). After a thorough taxonomic analysis, Harriman *et al.* (2011) did not find any traits that distinguished *C. v. vagabundus* larvae from other species of Ceratophylliae. Upon hatching, flea larvae are ~1.5mm, while fully developed larvae are 4 to 10mm (Wall & Shesarer 2001). Flea larva are generally not parasitic and feed on organic matrial, but some bird flea larvae have been found to be opportunistic parasites (Brinck-Lindroth & Smit 2007).

C. v. *vagabundus* has a typical flea life cycle, which includes three main stages: three in-star larvae stages, pupae and adult (Brinck-Lindroth & Smit 2007). In general the flea life cycle lasts three to four weeks but development is slowed by unfavorable conditions (Brinck-Lindroth & Smit 2007). Favorable conditions however are different between flea species because each species has a preferred temperature range, and deviations outside of that range can have adverse effects on growth and reproduction (Krasnov 2008). When the flea develops from the third in-star to the pupae stage it weaves a silken cocoon, which picks up debris from its environment that possibly acts as camouflage (Brinck-Lindroth & Smit 2007). Fleas can remain in their cocoon for extended periods of time

and are capable of withstanding environmental conditions much harsher than either adults or larvae (Wall & Shesarer 2001; Brinck-Lindroth & Smit 2007).

C. v. vagabundus spends the majority of their life in nests, with only adults leaving, primarily to feed on attending birds (Coulson *et al.* 2014; Lopez-Rull & Garcia 2015). This behavior is typical of avian fleas, most of which are dependent on the nests of their host. In fact, birds that do not return regularly to specific sites typically do not have fleas associated with them (Wall & Shesarer 2001). However, Bates & Rothschild (1962) found that some avian flea species routinely spend extended periods of time away from the nests as adults in search of new hosts.

2.3 Permission

Sysselmannen of Svalbard approved this study under the provisions of the Regulations for larger protected areas and bird sanctuaries in Svalbard of 2014, § 37 and the Svalbard Environmental Protection Act of 2001, § 37, in a letter (04062014) received on June 4th, 2014 and amended on June 10th, 2014. The project was also registered in the Research in Svalbard database (RiS ID: 6642).

2.4 Study design

Barnacle goose nests on Storholmen were visited approximately every second day from the 15th of June to the 11th of July 2014. Nests were accessed as part of the long-term monitoring and research projects of Prof. M.J.J.E. Loonen, University of Groningen, The Netherlands. All Barnacle goose nests on Storholmen were mapped and photographed between the 15th and the 18th of June.

2.4.1 *Flea dynamics*

In order to determine if fleas were overwinter on Storholmen, ten nest bowls that were unused in the 2014 season but were occupied the previous year were sampled. Soil samples were taken of the entire nest bowl, 5cm in depth. Samples were collected between the 2nd and the 4th of July.

Samples were extracted in the laboratory by first placing the samples in funnels leading to a vial of alcohol, and subsequently creating a heat gradient with 40-watt bulb lamps above the samples. Samples were left in the extraction apparatus for four days,

after which the vials of alcohol were sorted using a stereomicroscope. Prior to analysis the samples were stored between 2-6°C for no more than 25 days.

In order to explore the life cycle of the fleas during goose incubation, ten nests (the control nests from the experiment study) were sampled for fleas three times throughout this period. Nest samples were stored and extracted in the same way as the samples from the unused nest bowls. Since this was done as part of the experiment study, the methods are discussed in more detail below.

2.4.2 *Experimental study: hatching success*

To investigate the importance of fleas for the hatching success of geese, a manipulative field experiment was carried out. Ten nests were selected as controls and ten nests were treated with 3g of insecticide on two occasions (18th and 26th of June). The original study design was to have twenty nests in each group, but the project was downsized due to 'limited' approval of Sysselmanen of Svalbard. Nests were selected based on the highest amounts of blood spots and chosen from nests that had at least one ringed parent (Prof. M.J.J.E. Loonen, long term monitoring program). Nests were then paired based on similar amounts of blood spots and nest location, and subsequently assigned randomly to one of the two groups (control or treatment).

The insecticide that was used as the treatment was Beaphar 'Flea Repellent Powder' which is formulated for use on household pets. This insecticide repels fleas in two ways: 1) it desiccates the fleas and 2) it uses margosa extract as a natural pesticide. The main compound of margosa extract with insecticidal activity, azadirachtin acts as an insect feeding deterrent and growth regulator. It is critical that dangerous toxins are not introduced into the Arctic even for research proposes, and margosa extract was deemed a 'safe' insecticide because it breaks down rapidly in nature, and accumulation and long-distance transport is unlikely. Also, margosa extract has a low potential for bioaccumulation in aquatic and terrestrial organisms. It has low toxicity to birds, mammals, bees and plants. It has been found to be slightly toxic to fish and other aquatic organisms (Margosa Extract Assessment Report 2011).

All study nests were sampled for fleas three times by removing approximately 5x5cm samples of nest material and 5x5cm of soil below the nest. The first samples were taken at the beginning of incubation and before treatment was administered (June 18th).

The second set of samples was taken eight days after the treatment in the middle of incubation (June 26th). The final samples were taken after the geese abandoned their nests (between June 26th and July 7th). The samples were stored at 2-6°C for no more than 25 days.

Samples were stored and extracted in the same way as the samples from the unused nest bowls. Flea larva, pupae and adults from extracted samples were subsequently counted. Flea larvae were split into two classes based on size (small <3mm, large >3mm). Also, sample material was weighed after extraction.

In order to measure nest attendance of incubating birds, Thermochron iButton temperature loggers (Model DS1921G) were placed in the twenty study nests, on the 15th or the 18th of June. They were set to take a temperature reading every 3 min. The data was downloaded every visit to Storholmen (~ every 3 days) and the temperature loggers were immediately restarted and replaced in the nests. The loggers were placed under the eggs and above the nest material. Loggers were subsequently collected after the incubation was either completed or terminated. Additionally, Maginon trap cameras (Model WK 3 HD) were used to validate the temperature data (Appendix: Figure 6.2G). The trap cameras were placed 2-4m from the nest and were moved between nest pairs every three days. Also, all study nests were monitored through incubation for egg loss and hatching date.

2.4.3 *Blood spots as a proxy measure*

In order to evaluate the use of blood spots on the goose eggs as a proxy measure for flea infestations, all nests of ringed birds on Storholmen (102 nests in total) were photographed between the 16th and 18th of June (referred to as 'time 1' photos). A photograph was first taken of the nest from a standard distance of approximately 20cm (Appendix: Figure 6.2A). Subsequently each egg was individually removed from the nest and placed on a black background and photographed from the same standard distance. To assess changes in bloodspots over time a second set of photographs was taken on June 26th of only the twenty study nests (referred to as 'time 2' photos, Appendix: Figure 6.2B). Nests were assigned a percentage of blood coverage by visual assessment of the photos. The nest photos were primarily used in this process but when it was difficult to determine bloodspots in these photos the individual egg photos were also considered.

2.4.4 Observational study: colony hatching success and blood spots

Hatching success of all ringed geese nesting on Storholmen was monitored through incubation. The results were subsequently analyzed with the nest photos from 'time 1' in order to determine the relationship between goose egg hatching success and blood spots on the eggs.

2.5 Statistical analysis

All statistical analysis was conducted in R version 3.1.2 (2014-10-31) using Rstudio version 0.99.484 (R Core Team 2015). Data management was conducted in Microsoft Excel for Mac 2011 version 14.6.3 (Microsoft Office 2010).

2.5.1 Experimental study

2.5.1.1 hatching success

In order to assess the effect of the insecticide on the fleas, a paired Wilcox signed-ranked test was used to test the difference in the number of fleas found in the first samples of control and treatment nests (before the insecticide was administered). The prediction was that there would be no difference between the nests before the insecticide was added. Subsequently, a second paired Wilcox signed-ranked was used to test the difference in the number of fleas found in the samples after the insecticide was administered. This time the prediction was that there would be a difference because the insecticide would reduce the flea numbers in the treatment nests.

Hatching success of goose eggs was analyzed with a generalized linear mixed model (GLMM) with binomial distribution using the lme4 package (Bates *et al.* 2015). Goose eggs were classified as either success=1 or fail=0 and their outcome was modeled with treatment, larvae and adult fleas counts from the three sample periods, blood spots, hatch date, and clutch size as predictor variables and nest as a random variable (n=67, groups=20). The variables larvae and adult fleas were calculated by taking the sum of the fleas (larvae or adults) observed in all samples and dividing it by the sample weights. One nest was dropped from this analysis because it was predated by a polar bear.

2.5.1.2 nest attendance

The mean standard deviation for all temperature readings in a single day (~480 observations) was calculated (referred to as σ^{daily}). Subsequently, a mean standard deviation of the last ten days (when there was less than 10 days of data, as many days as possible were included) of incubation was calculated (referred to as $\sigma^{10\text{-}day}$).

$$\sigma^{10\text{-}day} = \mu \left(\sum_{i=1}^{10} \sigma^{daily} \right)$$

A standardized time until hatching was selected because geese change their nest attendance behavior as incubations progresses (Hepp *et al.* 2015). The end of incubation was determined with field observations, temperature data and trap camera photos.

In order to validate mean standard deviation of nest temperatures as a measure of nest attendance, female recess time was established for a 24-hour period by analyzing the photos from the trap cameras and comparing this to the corresponding σ^{daily} (n=20 on 17 different nests). Recess time was used to predict the σ^{daily} with a linear model. Two observations were identified as possible outliers, so the analysis was conducted again without these observations. A Shapiro-Wilk test for normality was conducted on the residuals of these models.

Two linear regression models were created with $\sigma^{10\text{-}day}$ as an explanatory variable and blood spots and larvae as predictor variables. The variable 'larvae' was calculated by taking the sum of flea larvae observed in all samples and dividing it by the sample weights. A Shapiro-Wilk test for normality was also conducted on the residuals of theses models.

A generalized linear mixed model (GLMM) with binomial distribution was created using the lme4 package in R (Bates *et al.* 2015). As before, goose eggs were classified as either success=1 or fail=0 and their outcome was predicted with the variable $\sigma^{10\text{-}day}$, and with nest as a random variable (n=67, groups=20).

***2.5.2** Blood spots as proxy for flea infestations*

In order to assess the use of blood spots as a proxy measure of flea infestations, two generalized linear models (GLM) with Poisson distribution and an offset variable, which was the logarithm of the sample weights (Zuur *et al.* 2009), were used to predict larvae

and adult fleas counts. The predictor variables in these models were blood spots, time of photo until hatching and an interaction term (n=20). Only observations from the first sample period were used, so treatment was not included in this model (both photos and samples were taken before the insecticide was administered to the treatment nests). Since the overdispersal parameter was very large for the models, new models were created with negative binomial distribution using the MASS package in R (Venables & Ripley 2002, Zuur *et al.* 2009). The best model was selected based on the AIC values. When a variable in the model with the lowest AIC value was not significant and AIC value was no less than two units of the reduced model the reduced model was preferred (Arnold 2010).

In order to assess how time affected the amount of blood covering the goose eggs, a paired Wilcox signed-ranked test was used to compare the percentages obtained from time 1 photos (taken 15-18th of June) to time two photos (taken 26th of June). Also, a linear model was created to predict change in blood spots by amount of blood spots at time 1. A Shapiro-Wilk test for normality was also conducted on the residuals of these models.

2.5.3 *Observational study: colony hatching success and blood spots*

Hatching success was analyzed for all eggs of ringed geese nesting on the Storholmen colony with a GLMM with binomial distribution (n=236, groups=73). Goose eggs were classified as either success=1 or fail=0 and their outcome was modeled with blood spots, clutch size, and hatch date as a predictor variables and nest as a random variable using the MASS package in R (Venables & Ripley 2002). All nests that received the insecticide treatment during the experiment were excluded from this analysis. The best model was selected based on the AIC values. When a variable in the model with the lowest AIC value was not significant and AIC value was no less than two units of the reduced model the reduced model was preferred (Arnold 2010).

3. Results

3.1 Flea dynamics

Fleas were found in three of the ten unused nest bowls. One sample had ten adult fleas, one sample had eleven larvae, and one sample had one adult and one larvae. No pupae were found in any of the unused nest bowls.

More adult fleas and pupae were found in the final sampling period than in the first. Only two pupae were found in the first sample period, while the remaining 72 were found in the second two sample periods (Figure 3.1A). The number of larvae found in the samples decreased as goose incubation progressed. However, at the end of nesting there were both large and small larvae. The proportion of large to small larvae remained similar throughout incubation (Figure 3.1B).

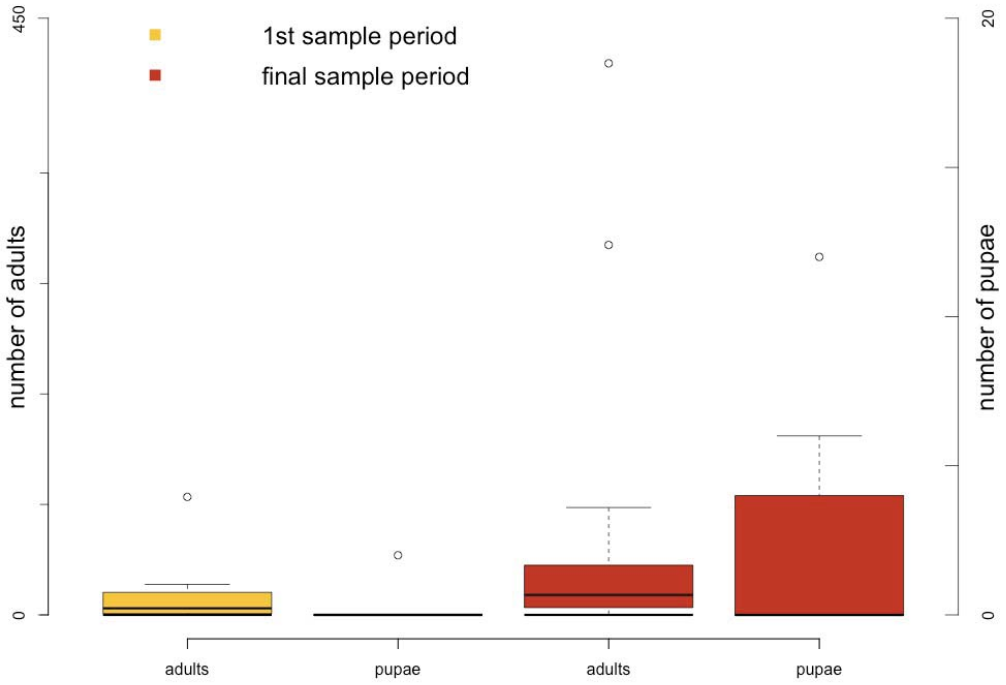

Figure 3.1A: Box-plots of the number of adult fleas (*Ceratophyllus vagabundus vagabundus*) and pupae extracted from Barnacle goose (*Branta leucopsis*) nest samples. Samples are from the first and the last sample periods and only of control nests (*n*=10). The left axis is for adult fleas and the right is for pupae. The first samples were taken on 18th of June 2014 and last samples were taken when the geese terminated incubation (between 26th of June and the 11th of July 2014).

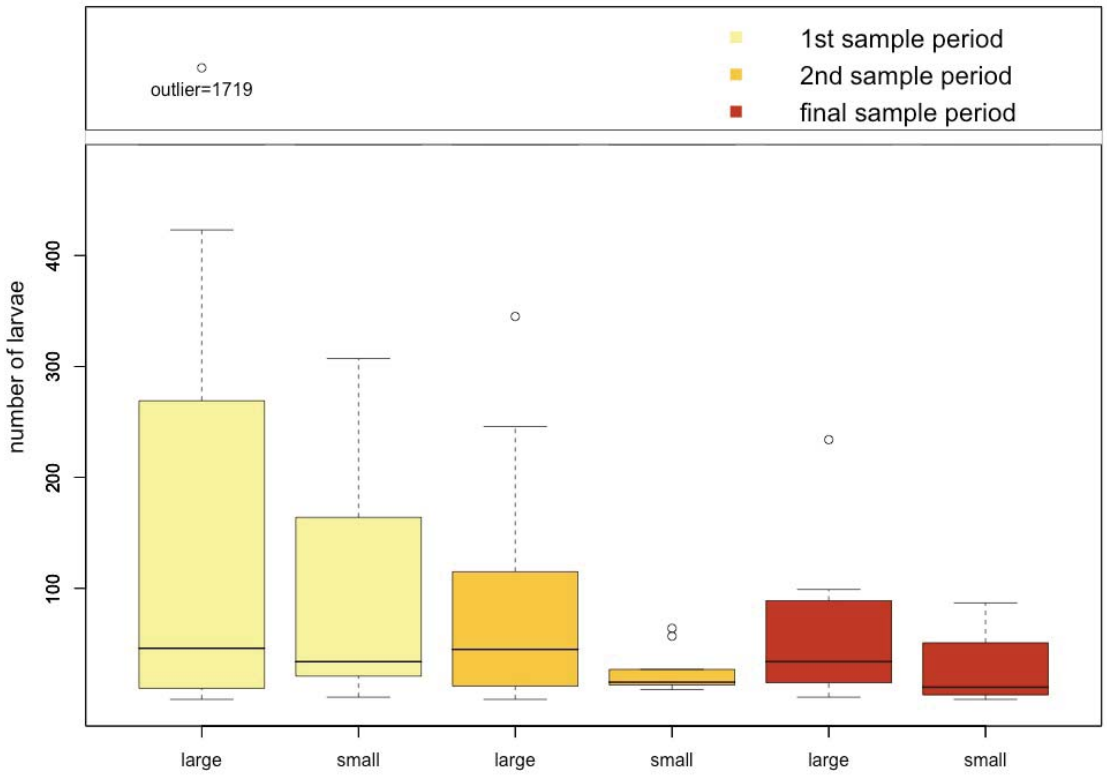

Figure 3.1B: Box-plots of the number of large and small flea larvae (*Ceratophyllus vagabundus vagabundus*) extracted from Barnacle goose (*Branta leucopsis*) nest samples. Samples are from each of the three sample periods and only of control nests (*n*=10). Larvae were classified as large when they were greater than 3mm and small when they were less than 3mm. The first samples were taken on 18th of June 2014, the second samples were taken on the 26th of June 2014, and the final samples were taken when the geese terminated incubation (between 26th of June and the 11th of July 2014).

3.2 Experimental study

3.2.1 Effect of insecticide flea populations

The insecticide had a measurable effect on larvae but not on adult fleas. There was not a significant difference between the number of larvae found in treatment and control nests before the insecticide was administered (P=0.971, W=51), but after the insecticide was administered control nests had significantly more larvae (P=0.002, W=83, Figure 3.2.1). However, there was not a significant difference between number of adult fleas found in control and treatment nests after the insecticide was administered (P=0.762, W=46).

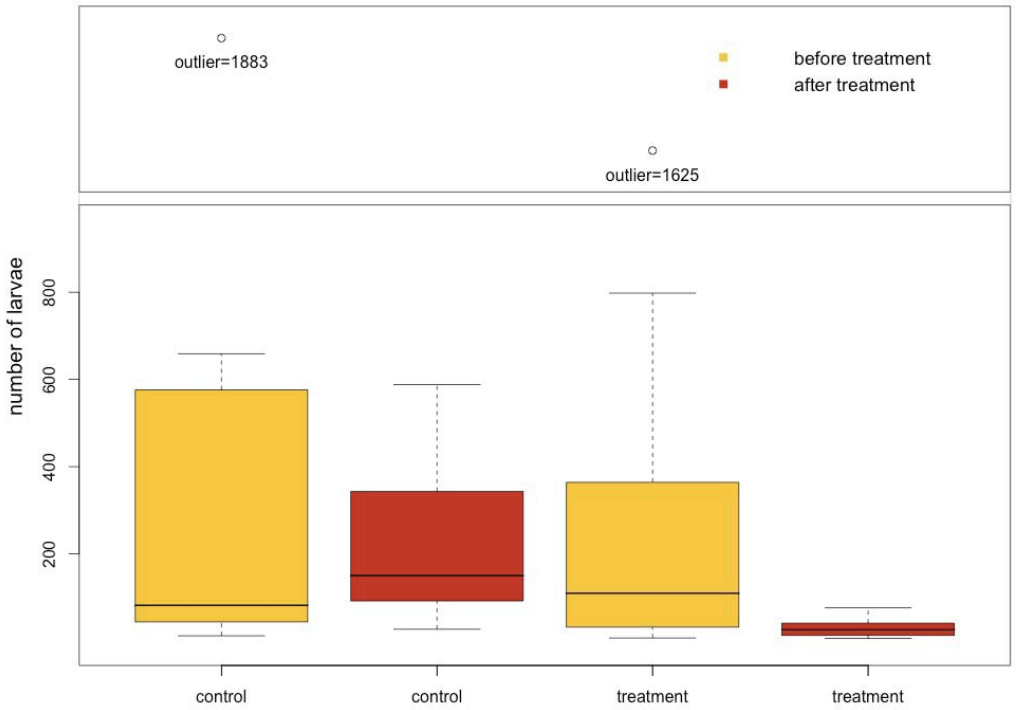

Figure 3.1.2: Box-plots of the number of flea larvae (*Ceratophyllus vagabundus vagabundus*) extracted from Barnacle goose (*Branta leucopsis*) nest samples before (yellow) and after (orange) insecticide was administered (*n*=20). Insecticide was administered to the ten 'treatment' nests in order to reduce the flea infestations while ten nests were left as controls. There were significantly fewer larvae in the treatment nests than the control nests after they were treated with the insecticide (P=0.002, W=83). The 'before treatment' samples were taken on 18th of June 2014, and the 'after treatment' samples were taken two times once on the 26th of June and once when geese terminated incubation (between the 26th of June and the 11th of July 2014).

3.2.2 Predicting hatching success

Goose egg hatching success was higher in nests that were treated with the insecticide, but this effect was only near significant (P=0.066, Table 3.2.2). Flea larvae were a significant negative predictor of goose egg hatching success (P=0.023). The model that predicted goose egg hatching success with the lowest AIC score had larvae, treatment and the interaction term larvae* treatment as predictor variables (AIC=62.4). However, the interaction term was only near significant (P=0.082) and AIC score was less than two of the reduced model so the reduced model was preferred (Table 3.2.2). Predictions were then made for the preferred model and can be seen in Figure 3.2.2. All other variables were dropped from the analysis because they were neither significant nor did their inclusion decrease the AIC score (see Appendix Table 6.1A for results from these models).

Table 3.2.2: Results from GLMMs with binomial distribution that predicted Barnacle goose (*Branta leucopsis*) egg hatching success with nest as a random variable (preferred model in bold). Ten nests were treated with an insecticide to reduce the number of fleas (*Ceratophyllus vagabundus vagabundus)* and this effect was accounted for with the variable 'treatment' (*n*=67, groups=20).

GLMM	Variable	Estimate	Std. Error	Pr(>|z|)	AIC
success ~ larvae + treatment + larvae * treatment + (1 | nest)	(Intercept)	2.807	1.073	0.009 **	62.4
	larvae	-0.029	0.011	0.013 *	
	treatment: T	0.242	1.288	0.851	
	larvae* treatment: T	0.022	0.013	0.082 .	
success ~ larvae + treatment (1 | nest)	(Intercept)	1.812	0.780	0.020 *	64.1
	larvae	-0.015	0.006	0.018 *	
	treatment: T	2.157	1.110	0.052 .	
success ~ larvae + (1 | nest)	(Intercept)	2.812	0.947	0.003 **	67.0
	larvae	-0.016	0.007	0.023 *	
success ~ treatment + (1 | nest)	(Intercept)	0.818	0.691	0.236	69.1
	treatment: T	2.356	1.282	0.066 .	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

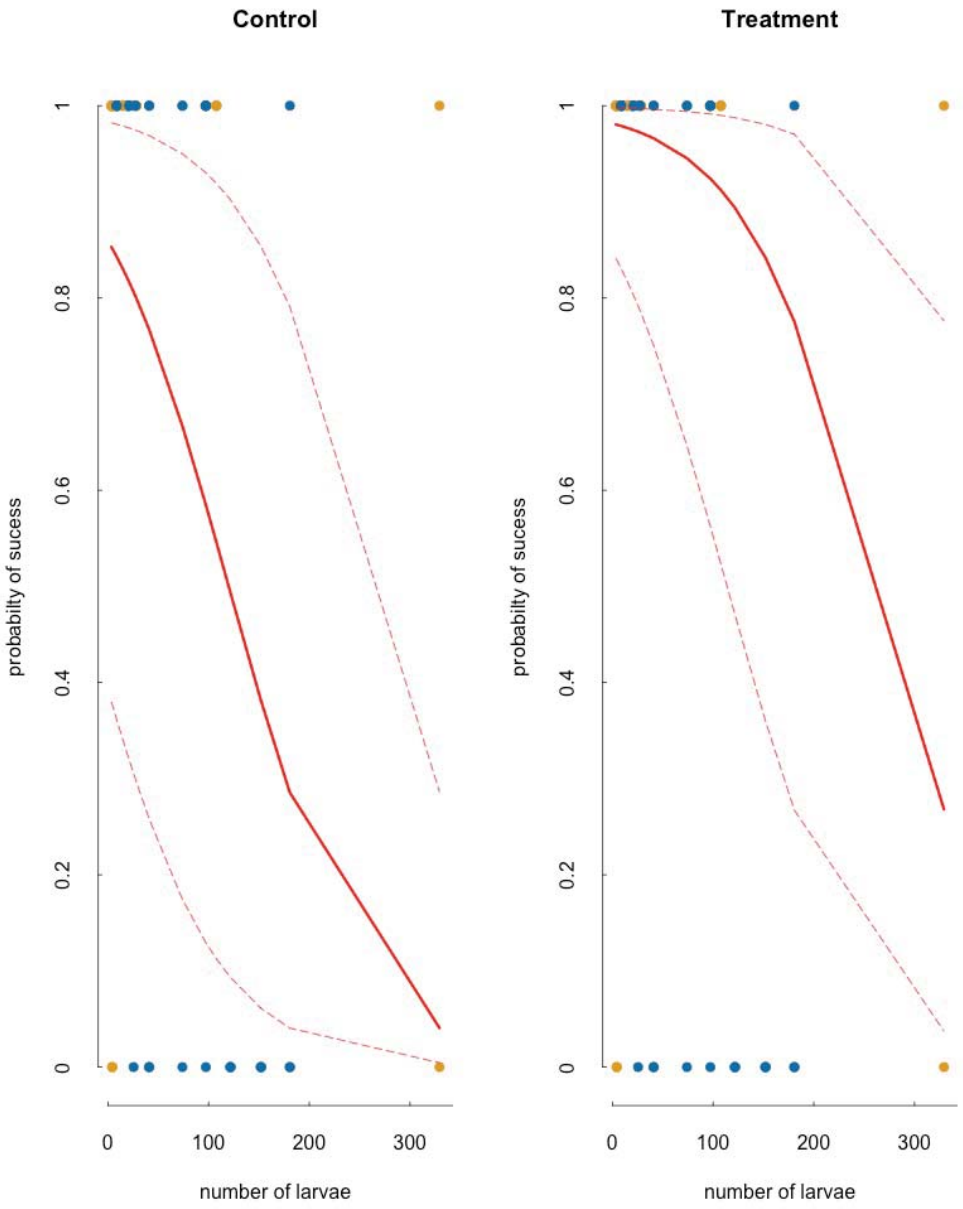

Figure 3.2.2: The probability a Barnacle goose (*Branta leucopsis*) egg will hatch (y) given a number of flea (*Ceratophyllus vagabundus vagabundus*) larvae found in the nest samples. The solid red line is predictions from a GLMM that predicted goose egg hatching success by the number of larvae found in the nest samples and weather or not the nests were treated with an insecticide to reduce flea infestaions and with nest as a random variable (Ps= 0.018 (larvae) and 0.052 (treatment), AIC=64.1, *n*=67, groups=20). The dashed red lines are the confidence interval. There are two different regression lines: one for nests that were controls (left plot) and one for nests that were treated with an insecticide (right plot). Circles are observations from the study. Blue circles are eggs from control nests and yellow circles are eggs from nests that were treated with an insecticide.

3.2.3 *Nest attendance*

The variable σ^{daily} (the standard deviation nest temperature over a 24-hour period) was found to be a significant positive predictor of female goose recess time (P<0.001, adj. R^2= 0.75, Figure 3.2.3A). When the possible outliers were removed σ^{daily} was still a significant predictor of recess time, but less of the variation in the observations was explained (P=0.022, adj. R^2= 0.24, see Appendix Table 6.1B for model output).

The variable $\sigma^{10\text{-day}}$ (the standard deviation nest temperature for the last ten days of incubation) was significantly predicted by blood spots and larvae (see Figure 3.2.3B, Ps= 0.028 and 0.001, adj. R^2= 0.20 and 0.47 respectively). Additional analysis showed that larvae were a significant predictor of $\sigma^{10\text{-day}}$ without the obvious outlier, whereas blood spots were not (Ps= 0.011 and 0.212 respectively, see Appendix Table 6.1B for results from these models). Furthermore, the variable $\sigma^{10\text{-day}}$ was found to be a near significant negative predictor of goose egg hatching success (P=0.051, see Table 3.2.3).

Table 3.2.3: The results from a linear model that predicted Barnacle goose (*Branta leucopsis*) nest temperature fluctuations over a 24-hour period (referred to as σ^{daily}) with incubating goose recess time for the same 24-hour period, which was calculated by analyzing photos from trap cameras place 2-4m from the nests (*n*=20, for 17 nests). Also, the results from another linear model that predicted nest temperature fluctuations for the last ten days of incubation (referred to as $\sigma^{10\text{-day}}$) with the number flea (*Ceratophyllus vagabundus vagabundus*) larvae found in nest samples or percent of goose eggs covered in blood (referred to as blood spots) (*n*=20). The results from a GLMM with binomial distribution that predicted goose eggs hatching success with $\sigma^{10\text{-day}}$ and nest as a random variable (*n*=67, groups=20).

Linear model	**Variable**	**Estimate**	**Std. Error**	**Pr(>|t|)**	**Adj R^2**
σ^{daily} ~ recess time	(Intercept)	-0.473	0.462	0.319	0.75
	recess time	0.015	0.002	4.85e-07 ***	
$\sigma^{10\text{-day}}$ ~ larvae	(Intercept)	1.976	0.109	5.17e-13 ***	0.44
	larvae	0.004	0.001	0.001 ***	
$\sigma^{10\text{-day}}$ ~ blood spots	(Intercept)	1.916	0.175	2.1e-09 ***	0.20
	blood spots	0.021	0.009	0.028 *	
GLMM					**AIC**
success ~ $\sigma^{10\text{-day}}$ + (1 | nest)	(Intercept)	7.685	3.321	0.025 *	66.8
	$\sigma^{10\text{-day}}$	-2.629	1.346	0.051 .	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

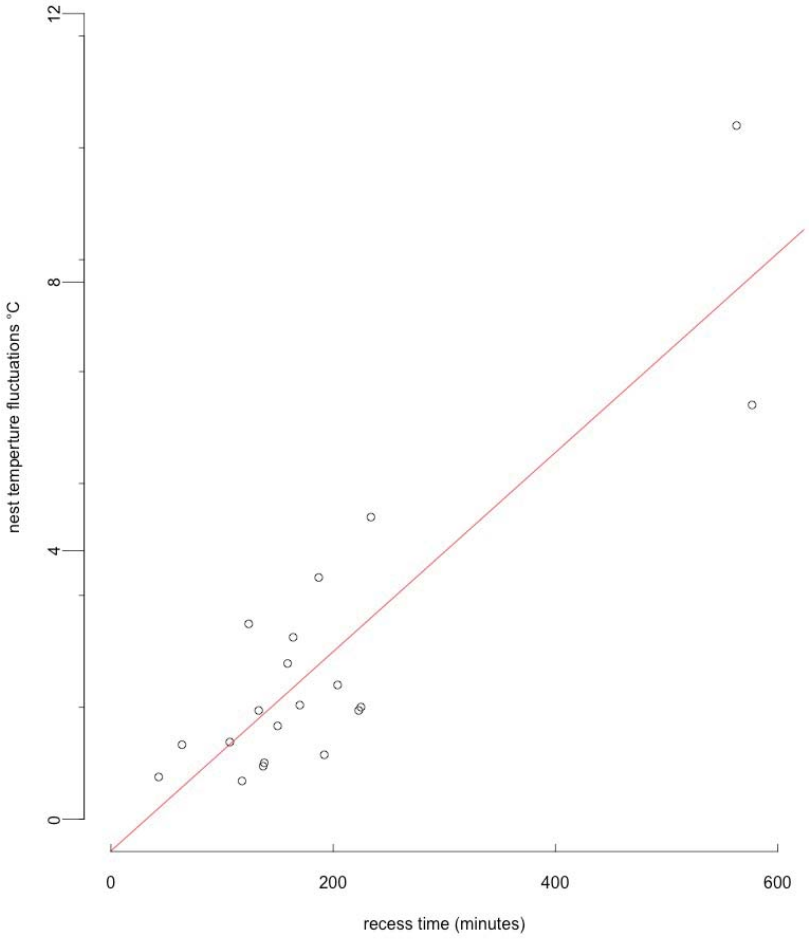

Figure 3.2.3A: Barnacle goose (*Branta leucopsis*) nest temperature fluctuations over a 24-hour period (referred to as 'σ^{daily}') recorded with temperature loggers located within the nests; plotted against incubating goose recess time for the same 24-hour period, which was calculated by analyzing photos from trap cameras place 2-4 meters from the nests. Circles are observations and the red line is a regression line with the equation: $\sigma^{daily} \sim -0.473+0.015$*recess time ($P>0.001$, adj. $R^2=0.75$, $n=20$ for 17 nests).

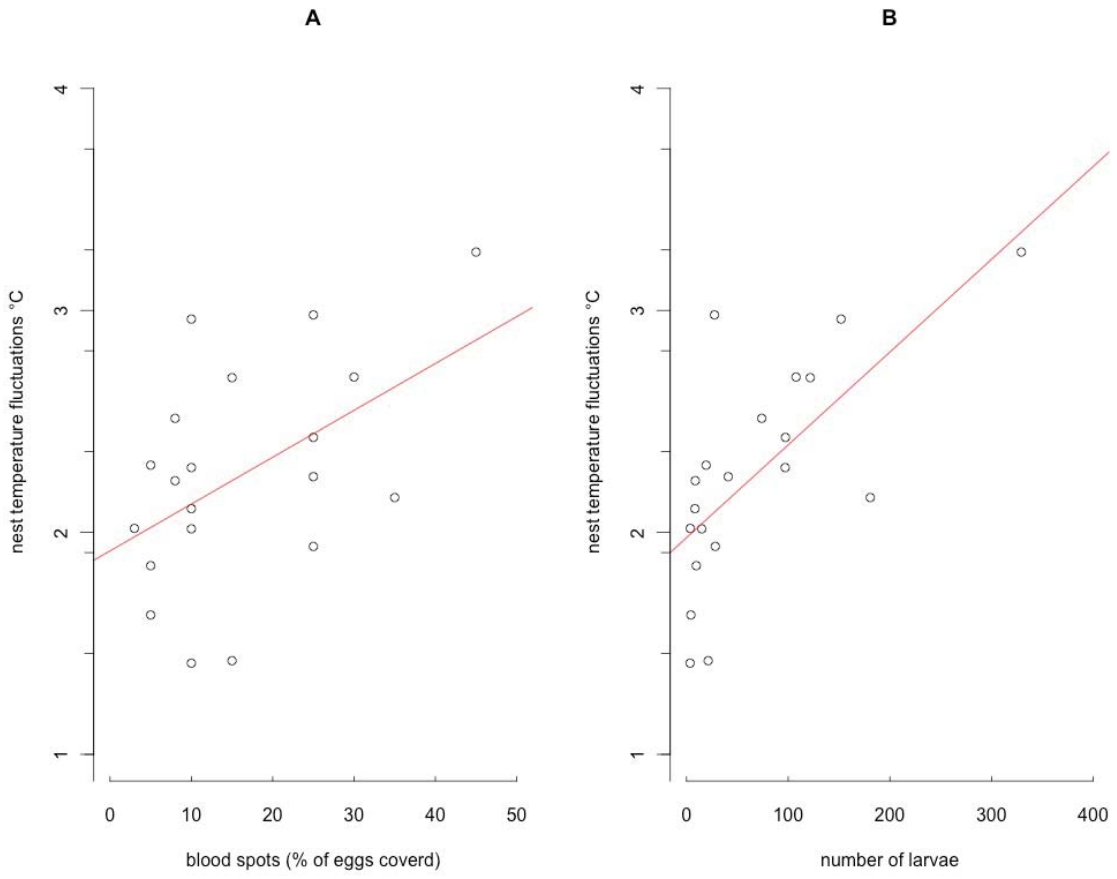

Figure 3.2.3B: Barnacle goose (*Branta leucopsis*) nest temperature fluctuations for the last ten days of incubation (referred to as $\sigma^{10\text{-day}}$) recorded with temperature loggers located within the nests; plotted against blood spots on goose eggs (plot A) and flea (*Ceratophyllus vagabundus vagabundus*) larvae extracted from nest samples (plot B). Circles are observations and the red line is a regression line with the equation for plot A: $\sigma^{10\text{-day}} \sim 1.916+0.21*$blood spots (P=0.028, adj. $R^2= 0.20$, *n*=20), and the equation for plot B: $\sigma^{10\text{-day}} \sim 1.976+0.004*$larvae (P=0.001, adj. $R^2=0.47$, *n*=20).

3.3 Blood spots as a proxy measure

3.3.1 Predicting fleas with blood spots

Blood spots were significant positive predictors of both larvae and adult fleas (Table 3.3.1 and Figure 3.3.1). The variable 'time' (the time from when the photo was taken until goose eggs hatched) was dropped from the analysis because it was not significant and did not reduced the AIC score (see Appendix Table 6.1C for results from this model).

Table 3.3.1: The results from two GLMs with negative binomial distribution that predicted flea (*Ceratophyllus vagabundus vagabundus*) larvae or adults that were collected in the first Barnacle goose (*Branta leucopsis*) nest samples (taken June 18, 2014) with the percent of goose eggs covered by blood in that nest (referred to as 'blood spots') as the predictor variable, and with the logarithm of the sample weights as an offset variable (*n*=20).

Negative Binomial GLM	Variable	Estimate	Std error	Pr(>|z|)	Dispersion parameter	~R^2	AIC
larvae ~ blood spots, offset(log(sample weight))	(Intercept)	2.376	0.347	7.72e-12 ***	1.146	0.53	254.3
	blood spots	0.088	0.018	1.36e-06 ***			
adult ~ blood spots, offset(log(sample weight))	(Intercept)	-0.890	0.455	0.051 .	0.787	0.45	129.6
	blood spots	0.093	0.023	5.19e-05 ***			

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

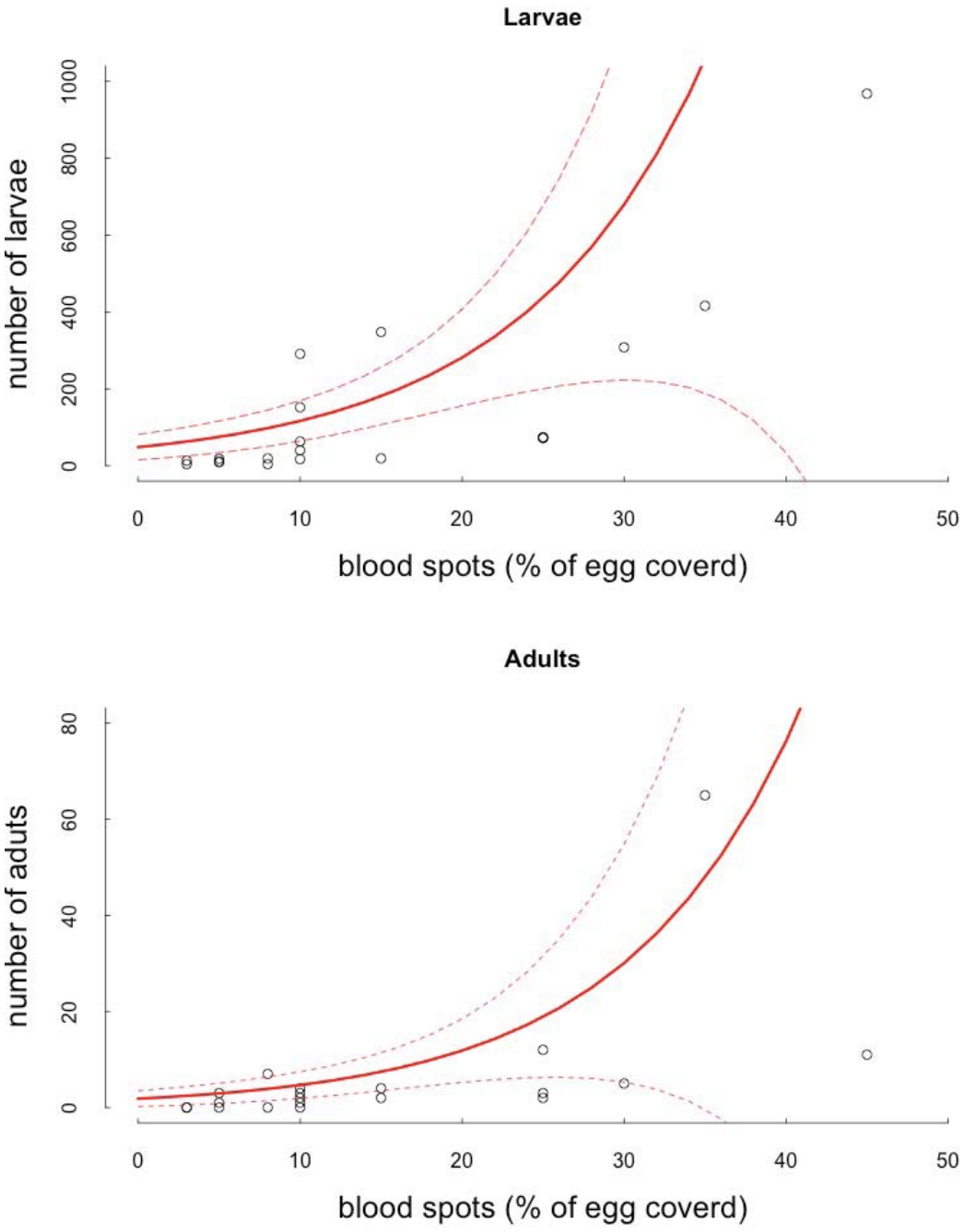

Figure 3.3.1: Predictions (solid red line) from two GLMs (with negative binomial distribution) with flea (*Ceratophyllus vagabundus vagabundus*) larvae (top plot) and adults (bottom plot) as the response variables (y) and percent of goose eggs covered by blood (referred to as 'blood spots') as the predictor variable (x), and with the logarithm of the sample weight as an offset variable (Ps<0.001 and <0.001, ~R^2s= 0.53 and 0.45 respectively, *n*=20). Samples were collected on June 18, 2014 from Barnacle goose (*Branta leucopsis*) nests. The open circles are observations and the dashed red line is the confidence interval. **Note: observations have varying sample weights and predictions were made with the mean sample weight, so predictions are more accurate than they appear.**

3.3.2 Blood spots over time

There was a significant decrease in blood spots from time 1 photos to time 2 photos representing a gap of 10-12 days (Figure 3.3.2A, P=0.002, V=89.5, *n*=20). It also appeared that blood spots wore off more rapidly on eggs with more blood coverage (Figure 3.3.2B). There was a significant linear relationship between the reduction of blood spots (difference between 'time 1' and 'time 2' blood spots) and the amount of blood on the eggs (P<0.001, R^2= 0.69, *n*=20).

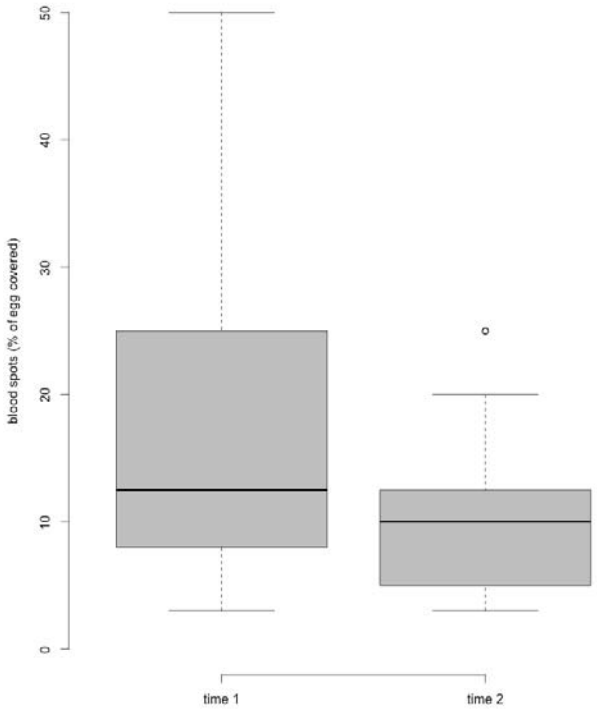

Figure 3.3.2A: Box-plots of the percent of Barnacle goose (*Branta leucopsis*) eggs covered by blood (referred to as blood spots) assessed from two sets of photos. The first set of photos was taken between 16-18th of June 2014 (referred to as 'time 1') and a second set was taken on 26th of June 2014 (referred to as 'time 2'). A paired Wilcox signed-ranked test showed a significant decrease in blood spots from time 1 to time 2 (P=0.001, V=89.5, *n*=20)

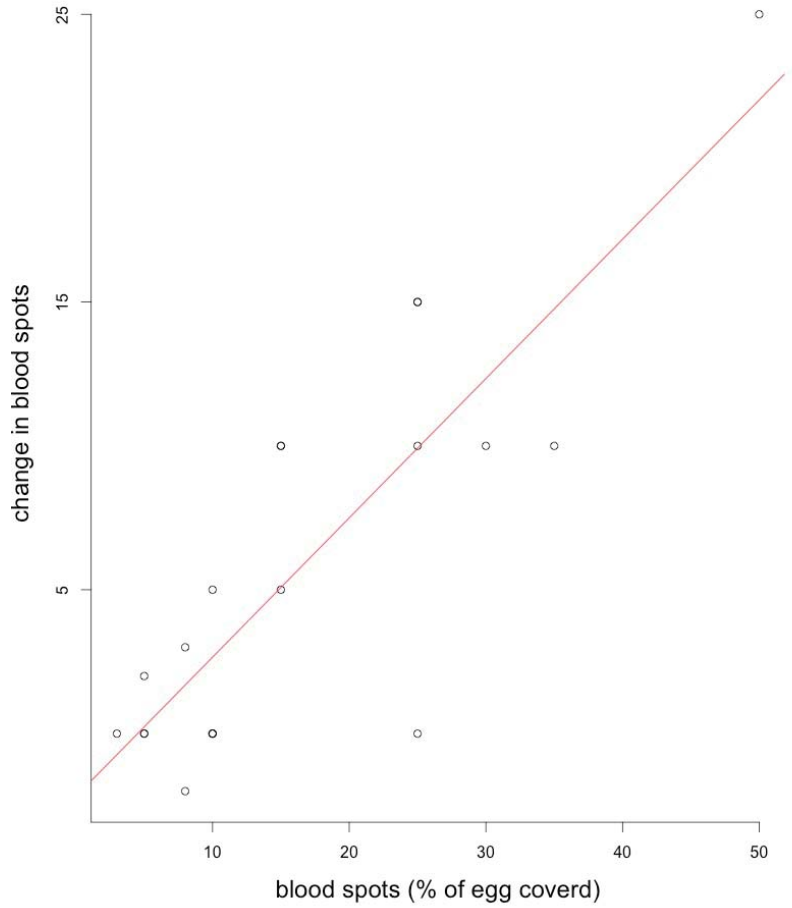

Figure 3.3.2B: The change in the percent of Barnacle goose (*Branta leucopsis*) eggs covered in blood (referred to as change in blood spots) over the course of 10-12 days (y) plotted against the percent of blood covering the eggs (referred to as blood spots) during the original observation (x). The circles are observations and the red line is a regression line with the equation:
change in blood spots ~ -2.187+0.484*blood spots ($P<0.001$, adj. $R^2= 0.69$, $n=20$).

3.4 Observational study: colony hatching success and blood spots

Blood spots were a significant negative predictor of goose egg hatching success in the Storholmen colony (Table 3.4). However, this model had low predictive power (Figure 3.4). All other variables were determined not to improve the model (see Appendix Table 6.1D for further results).

Table 3.4: The results from a GLMM with binomial distribution that predicted Barnacle goose (*Branta leucopsis*) egg hatching success with percentage of the egg covered by blood (referred to as 'blood spots') and with nest as a random variable for all ringed geese nesting in the Storholmen colony (*n*=236, groups=73)

GLMM	Variable	Estimate	Std. Error	Pr(>|z|)	AIC
success ~ blood spots + (1 | nest)	(Intercept)	3.953	0.609	>0.001***	162.1*
	blood spots	-0.155	0.049	0.002**	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001
*Note: since MASS package does not report an AIC for GLMMs this AIC was obtained from the same model but with lme4 package.

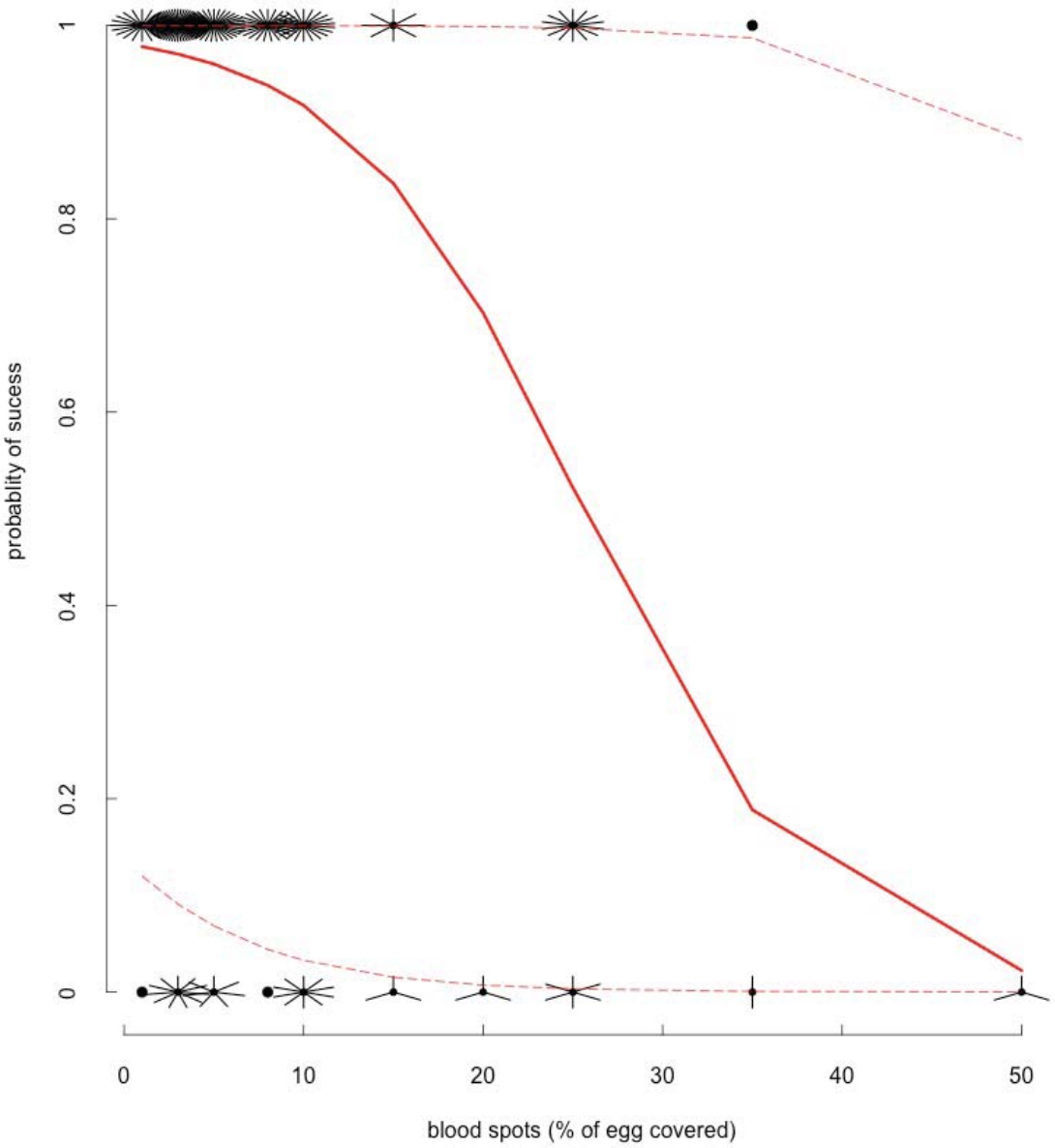

Figure 3.4: The probability that a Barnacle goose (*Branta leucopsis*) egg will hatch (y) given percentage of the egg covered by blood (referred to as 'blood spots'). The solid red line is predictions from a GLMM that predicted goose egg hatching success by blood spots for all ringed geese nesting in the Storholmen colony (P= 0.002, *n*=236, groups=73). The dashed red lines are the confidence interval and circles are observations (the number of lines radiating from the circles represent the total number of observations at that point).

4. Discussion

4.1 Flea dynamics

Evidence from this study indicates that fleas were overwintering in Svalbard. Fleas were found in samples taken from unused nest bowls and evidently overwintered there from the previous summer when the nest bowl had been occupied by geese. Also, the majority of pupae were found in the final nest samples (taken just after the geese had abandoned the nests) and were likely the overwintering stage. Furthermore, the final nest samples contained the most adult fleas, which may have been pupae that developed into adults during the extraction process.

These findings are supported by other research. Harrium *et al.* (2011) stated that *C. v. vagabundus* overwinters 'presumably' as pupae in old nest material (down and vegetation). Also, a study conducted on the flea, *Ceratophyllus idius*, found that 32% of adults survived laboratory cooling down to -30°C (Schelhaas & Larson 1989). Prof. M. J.J.E. Loonen found few fleas on Barnacle geese nesting on Storholmen during a dust ruffle study conducted late in the summer when geese were molting (*unpublished data*). Furthermore, Bird fleas from the family Ceratophyllidae do not live on the host body but rather in the nest of the host (Wall & Shesarer 2001, Harriman *et al.* 2008; Tripet *et al.* 2002; Marshall 1981; Lehane 1991). It would therefore be surprising for fleas, which are not adapted to life on birds, to be able to survive the migration to the Arctic each year in substantial numbers.

However, fleas overwintering in Svalbard have considerable challenges. Schelhass and Larson (1988) noted that the ability of *C. idius* to supercool did not enhance survival at -6°C in field trials. The annual mean air temperature in Svalbard is -6.7°C and mean winter air temperatures fall below -15°C (Gwiazdowicz *et al.* 2012). In both of the above examples (Harrium *et al.* 2011; Schelhaas & Larson 1989), fleas were overwintering in old nest material, while in Svalbard, due to the lack of vegetation the fleas would have to overwinter in the soil.

Although the harsh environment of Svalbard presents major challenges, results from this study along with the current understanding of *C. v. vagabundus* ecology strongly support the conclusion that fleas are overwintering in Svalbard. It has been

shown that snow cover is important for overwintering invertebrates in Svalbard because it insolates from minimum temperatures as well as short-term fluctuations (Coulson *et al.* 1995). Kongsfjorden experienced more snow in spring of 2014 than typical (Norwegian Meteorology Institute 2014) and this may have increased survival during the wintering. Climate change projections include warmer conditions and more snow in the Arctic (IPCC 2013), and Descamps (2013) found that warmer winter temperatures explained an increase in ectoparasites in Arctic seabird colonies. Therefore, it is possible that flea infestations will also increase on Storholmen; however, long-term studies need to be done in order to further explore this phenomenon.

Pupae are the common overwintering stage for fleas (Riding & Belthoff 2015), but in this study evidence suggests that *C. v. vagabundus* may also be capable of overwinter as larvae in some years. This is in contrast to general knowledge of fleas, which suggests both adults and larvae are not resistant to environmental extremes (Wall & Shearer 2001), and in contrast to the results from Harriman *et al.* (2008) study that found no *C. v. vagabundus* larvae in nests surveyed early in incubation. This study found two cohorts of larvae, which were easily recognized in the samples due to the size difference between the cohorts. The small larvae likely hatched this season while the large larvae may have overwintered. Also, both large and small larvae were found in the final nest samples. The large larvae may pupate before winter, but the small larvae likely attempt to overwinter in their current stage. Furthermore, larvae were found in the unused nest bowl samples. This suggests that *C. v. vagabundus* may be capable of a two-year life cycle in the High Arctic.

Arctic adapted life cycles have been shown in other insects including semivoltine (life cycles that take more than one year to complete) life histories (Strathdee *et al.* 1993; Bale *et al.* 1997; Taylor *et al.* 2010). Danks (1992) noted that semivoltine life histories in insects are correlated with environmental stressors such as cold and unpredictable temperatures as well as variable food supplies. The High Arctic is known for both cold and unpredictable temperatures and geese do not occupy nest bowls every season. However, no literature was found regarding multi-year life cycles in fleas, and the evidence to support this finding is somewhat circumstantial. Therefore, it is important to

note this observation, but it needs to be further investigated before any conclusions are drawn.

4.2 Experimental study

4.2.1 Hatching success

The insecticide applied in the field experiment had a significant effect on larvae but not on adults fleas, and larvae counts from nest samples were a better predictor of goose egg hatching success than adult flea counts. This finding is counterintuitive because adult fleas primarily drive the costs to their hosts (Wall & Shesarer 2001). Although flea larvae have been documented to be opportunistic parasites (Brinck-Lindroth & Smit 2007), this is not a common event and there was no indication that this occurred during the study. The number of adult fleas found in each sample varied dramatically between sample periods for the same nests. Nest samples were small in size and adult fleas are highly mobile, so it is likely that adult fleas avoided capture during collection or escaped during extraction. The best explanation for these findings is that larvae counts were a more accurate measure of flea infestations. It can then be presumed that treatment had an effect on adults as well as larvae and adult fleas drove the decrease in goose egg hatching success.

Goose egg hatching success increased in nests that were treated with the insecticide although this was only approaching significance (P=0.066). Also, the best model that predicted hatching success included both larvae and treatment as predictor variables. Considering the small sample size and a limited amount of insecticide used, these results provide strong experimental evidence to support the conclusion that fleas were having a negative impact on goose egg hatching success.

These findings are also supported by other research. An observational study in the Canadian Arctic found that flea abundances were a negative predictor of nest success of Ross's and Lesser Snow Geese (Harriman & Alisauskas 2010). Other studies have shown that fleas affect breeding success as well as reduce survival of nestlings of altricial birds (hatchlings are featherless and blind) (Oppliger *et al.* 1994; Fitze *et al.* 2004; Richner *et al.* 1993; Starck & Ricklefs 1998). This is, however the first study to experimentally demonstrate the negative effects of fleas on hatching success of wild precocial birds in the Arctic.

Harriman & Alisauskas (2010) hypothesized that blood spots on goose eggs could reduce gas exchange and cause the eggs to fail. While this remains a valid hypothesis, the goose eggs found in Harriman & Alisauskas (2010) study had much higher amount of blood cover than was found in this study. It would be necessary to do a manipulative study on goose eggs in order to determine the effect of blood spots on gas exchange. While this would be interesting, it does not alter the finding that heavy flea infestations are negatively impacting hatching success.

Booth *et al.* (1993) experimentally showed that ectoparasites can reduce their host's condition through the accumulation of 'subtle energetic costs' and Black *et al.* (2014) found that female geese usually sacrificed breeding attempts in favor of self-preservation by abandoning the clutch and proceeding with their molt early in the season. This gives one possible explanation for reduced hatching success. However, only one nest was abandoned entirely. This suggests that altered nest attendance may have also been an important contributing factor to the reduced hatching success observed in this study.

4.2.2 *Nest attendance*

It was found that standard deviation of nest temperatures over the course of a 24-hour period (σ^{daily}) was significantly predicted by incubating female recess time for the same period. Studies have shown that temperature loggers are effective at documenting incubation behavior by recording temperature fluctuations, which correspond to when the bird is on or off the nest (Hartman & Oring 2006; Mougeot *et al.* 2014; Arnold *et al.* 2006). Although many of these studies use more detailed analysis of the temperature data, they were carried out in environments where temperature could be near or even above incubation temperatures and in areas with pronounced diurnal patterns. Due to the conditions of the High Arctic the ambient temperatures during this study were well below incubation temperatures and there was no diurnal patterns. This seems to have resulted in rapid drops in nest temperature when the incubating bird was away, and allowed for a simple analysis of the data.

The temperature fluctuation for the last ten days of incubation ($\sigma^{10\text{-}day}$) was a significant predictor of flea infestations and a near significant predictor of goose egg

hatching success (P=0.051). It can be concluded that incubating geese with heavily infested nests had reduced nest attendance and this had an impact on hatching success.

Reduced nest attendance likely resulted from agitation caused by adult fleas bites and increased foraging time to compensate for energetic loses inflicted by the fleas. Preening is the most common defense against ectoparasites, but the energetic cost can be twice that of the basic metabolic rate (Clayton *et al.* 2010). Incubating birds have to balance self-maintenance with the thermal requirements of the developing eggs (Hepp *et al.* 2015). It has been documented that female Barnacle geese with reduced body condition spent more time off the nest foraging, and this increases the risk of nest failure (Black *et al.* 2014). Even small reductions in incubating temperature can have large impacts on hatching success. Low incubating temperatures slow down development, reduces the 'quality' of the hatchlings, and increases the chances of predation (Tombre & Erikstad 1996; Hepp *et al.* 2006; Martin *et al.* 2007; DuRant *et al.* 2012; Hepp *et al.* 2015).

4.3 Blood spots as a proxy measure

Blood spots on goose eggs were a significant predictor of both larvae and adult fleas. These findings are supported by Harriman *et al.* (2008) who found that the proportion of eggs covered in blood had a positive correlated with adult fleas found in the nests.

The fact that the models had a large confidence interval for nests with many blood spots can be explained by the lack of observations with over 30% coverage. Also, it is important to note that the models were predicting flea infestations from a small sample (5x5cm) taken only once during incubation (the additional samples were not included in the analysis because treatment was administered after the first sample). If larger nest samples were taken and more samples from nests with over 30% coverage were included, then the model would likely produce better predictions.

Most of the blood spots appeared early in goose incubation and were subsequently worn off as incubation progressed. These findings are also supported by Harrima *et al.* (2008) who found that goose incubation stage at the time of blood spot assessment was significant in their models that predicted flea infestation with blood spots. In contrast to this, this study found that inclusion of time from when the photo was taken until goose eggs hatched did not improve the model that predicted flea infestations from blood spots.

It is therefore suggested that the percent of eggs covered by blood spots is a good proxy measure of flea infestations, but incubation stage at the time of blood spot assessment should be considered.

4.4 Observational study: colony hatching success and blood spots

Blood spots were a significant negative predictor of goose egg hatching success in the Storholmen colony. These results were also in accordance with the findings of the experimental study (see Figures 3.4 and 3.2.2). Together these findings give strong evidence supporting the conclusion that heavy flea infestations were having a negative impact on goose egg hatching success.

This study only considered the effect of fleas on goose egg hatching success; however, negative effects of ectoparasites after hatching have also been documented (Fitze *et al.* 2004; Richner *et al.* 1993; Hanssen *et al.* 2013). Although these studies have primarily been conducted with altricial birds, it nevertheless suggests that the effect of the ectoparsites at the population level is likely higher than the findings of this study. In order to explore the effects of fleas on the Barnacle goose population, a multi-year study would be needed.

Although, it has been shown that scaling the impacts of parasites from an individual level to population level can be difficult (Pedersen & Fenton 2015), some population level trends can be inferred based on these findings. Black *et al.* (2014) noted strong negative density-dependent effects in offshore island colonies in Svalbard, which they attribute to competition and 'events' during incubation periods. Increased flea infestations could also explain this finding. As discussed above, the results from this study suggest that fleas were both overwintering in nest bowls and impacting goose egg hatching success. The simplest way to deal with parasites is to avoid them and nest site selection is one way to avoid ectoparasites, but for many species good nest sites are scarce (Lopez-Rull & Garcia 2015). As the colony increases in numbers and age, fewer nest sites are available and fleas likely have accumulated in some nest bowls. Therefore, the fleas may be influencing both local nest site selection and dispersal patters of geese.

Harriman *et al.* (2010) concluded that their study colony would experience population declines as a result of flea infestations if the average blood coverage reached 40% or higher. This study also found that the main reduction in goose egg hatching

success came from heavily infested nests. However, the findings of this study indicate a complex relationship between the geese and the fleas that may encompass multiple trophic levels and therefore may not be simple to predict. A multi-year study would be necessary to better explore this relationship.

Finally, it is important to note that these results illustrate the simplicity and power of using blood spots as a proxy measure for flea infestations. The amount of time and effort used to collect, extract, and sort samples from the 20 study nests would not have been feasible for the entire colony. The photos were taken only one time, as opposed to the three nest samples and did not involve any changes to the nest, so this was also a less invasive method. The use of blood spots as a proxy measure for flea infestations will allow future studies the possibility of focusing on larger population impacts of fleas while reducing disturbance to parasite and host.

4.4.2 Polar bear visit

A polar bear visited the Storholmen colony at the end of incubation and predated one of the study nests as well as other Barnacle goose nests and Common Eider duck nests. Polar bears visiting goose colonies during nesting is a behavior that is increasingly being observed (Drent & Prop 2008; Rockwell & Gormezano 2009; Stirling 2011; Iverson *et al.* 2014). It has been suggested that this behavior is related to climate change and phenological match and mismatch. The bears cannot access breeding seals due to reduced sea ice and venture onto land while the geese are nesting (Drent & Prop 2008; Rockwell & Gormezano 2009). Although this was an isolated event on Stoholmen, polar bears have long memories and visits could become common occurrences. Impacts of this behavior for either the geese or the bears are outside the scope of this study, but documentation of this event is useful for future research. Furthermore, while this event had little to do with fleas, it underlines the complex and dynamic nature of even 'simple' Arctic ecosystem interactions and the far-reaching effects of climate change.

4.5 Limitations

It is possible that the insecticide used during this study had an effect on other Barnacle goose ectoparasites. Other ectoparasites that have been documented to infest Barnacle geese in Svalbard include the following: three species of lice (*Trinoton anserinum,*

Anaticola anseris, and *Ornithobius hexophthalmus*) and some mites (*Acari*: Prostigmata and Astigmatina) (Mehl *et al.* 1982; Pilskog *et al.* 2014).

The insecticide was only administered to the nests of the Barnacle Geese, so it is unlikely it impacted ectoparasites on the adult birds. Lice (Phthiraptera) typically spend their entire lives on their hosts and have not been documented in the nests of Barnacle geese (Lopez-Rull & Garcia 2015; Pilskog *et al.* 2014), and it can be assumed were not affected by the insecticide. Although adult mites that parasitize birds primarily live on their hosts, most nymph stages reside in nests (Lopez-Rull & Garcia 2015). It is likely that the insecticide had an effect on all invertebrates within the nests. It may have affected nymph stages of parasitic mites reducing their loads later in the season. Heavy infestations of mites have been shown to reduce breeding success of birds (Moller 1990).

The possibility that the results of this study were affected by the accidental reduction of mites cannot be entirely ruled out. However, in terms of numbers *C. v. vagabundus* was found to be by far the dominant ectoparasite in Barnacle goose nests in Svalbard (Pilskog *et al.* 2014), and Pilskog *et al.* (2014) found few parasitic mites in high Arctic nests. The finding from the observational study supported the results of the experimental study, showing that flea infestations (as measured by blood spots) were a significant predictor of hatching success (see Figures 3.4 and 3.2.2). Therefore, it is concluded that the principle effect measured in this study was a result of a reduction in flea infestations.

Another limitation of this study is that it only encompasses a single breeding season. Multi-year studies are critical for understanding complex and dynamic relationships in ecosystems. Weather data suggests that the summer of 2014 may have been a heavy snow year (Norwegian Meteorology Institute 2014). This could have had impacts on both the flea and goose communities as well as interactions between them. In order to assess the long-term effects of flea infestations on the colony or the impact of climate change on this system, a multi-year study would be necessary.

Finally, the sample size in the experimental study was small as a result of limited approval by Sysselmannen of Svalbard. Although a small sample size is a major limitation, the results of the experimental study were supported by the larger observational study. As discussed above, taken together these results provide strong

evidence for the conclusion that fleas had a negative impact on Barnacle goose egg hatching success.

4.6 Conclusion

This study found evidence of fleas overwintering in Svalbard, as well as some evidence that indicated *C. v. vagabundus* might be capable of a two-year life cycle in the High Arctic. These findings have important implications for predictions regarding the impact of flea infestations on the Storholmen colony as well as how this system will respond to climate change. It was also determined that blood spots were a good proxy measure of flea infestations, but become less accurate through incubation due to wear from incubating birds. It was then illustrated in the larger observational study that blood spots are a powerful tool for estimating flea populations. The findings from the experimental study and the larger observational study demonstrated that heavy flea infestations had a negative impact on the hatching success of Barnacle goose eggs. One important mechanism for this impact was that heavy infestations appeared to reduce nest attendance of incubating females. Based on these findings, it is suggested that researchers interested in either reproductive success or incubation behavior of Barnacle geese should include a measure of flea infestations in their studies and using blood spots as a proxy measure is a simple and disturbance-free method of doing this.

5. References

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6. Appendix

6.1 Additional analysis

Table 6.1A: (Table 3.2.2 with additional variables) Results from GLMMs with binomial distribution that predicted Barnacle goose (*Branta leucopsis*) egg hatching success with nest as a random variable. Ten nests were treated with an insecticide to reduce the number of fleas (*Ceratophyllus vagabundus vagabundus)* and this effect was accounted for with the variable treatment (*n*=67, groups=20).

GLMM	Variable	Estimate	Std. Error	Pr(>|z|)	AIC
success ~ larvae + treatment + clutch + hatch date + larvae * treatment + (1 | nest)	(Intercept)	1058.6909	1811.6619	0.5618	NA
	larvae	-0.0306	0.0103	0.0048	
	treatment: T	0.6025	1.4996	0.6935	
	clutch	-0.3619	0.6320	0.5754	
	hatch date	-0.0649	0.1115	0.5692	
	larvae* treatment: T	0.0202	0.0128	0.1343	
success ~ larvae + hatch date + (1 | nest)	(Intercept)	6.093e+02	1.891e+03	0.7473	68.9
	larvae	-1.642e-02	6.428e-03	0.0106 *	
	hatch date	-3.731e-02	1.163e-01	0.7484	
success ~ larvae + clutch + (1 | nest)	(Intercept)	4.728821	3.110282	0.1284	68.5
	larvae	-0.018245	0.008171	0.0256 *	
	clutch	-0.495359	0.724752	0.4943	
success ~ blood spots + (1 | nest)	(Intercept)	3.07752	1.40593	0.0286 *	71.7
	blood spots	-0.06978	0.05606	0.2132	
success ~ adult fleas + (1 | nest)	(Intercept)	2.42883	0.96269	0.0116 *	71.4
	adult fleas	-0.12130	0.08966	0.1761	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

Table 6.1B: (Table 3.2.3 without outliers) The results from a linear model that predicted Barnacle goose (*Branta leucopsis*) nest temperature fluctuations over a 24-hour period (referred to as σ^{daily}) with incubating goose recess time for the same 24-hour period, which was calculated by analyzing photos from trap cameras placed 2-4m from the nests (*n*=20, for 17 nests). Also the results from another linear model that predicted nest temperature fluctuations for the last ten days of incubation (referred to as $\sigma^{10\text{-}day}$) with the number of flea (*Ceratophyllus vagabundus vagabundus*) larvae found in nests samples or percent of goose eggs covered in blood (referred to as blood spots) (*n*=20). The results from a GLMM with binomial distribution that predicted goose eggs hatching success with $\sigma^{10\text{-}day}$ and nest as a random variable (*n*=67, groups=20).

Linear model	Variable	Estimate	Std. Error	Pr(>|t|)	Adj R^2
σ^{daily} ~ recess time	(Intercept)	0.116	0.697824	0.8696	0.2389
	recess time	0.011	0.004299	0.0229 *	
$\sigma^{10\text{-}day}$ ~ larvae	(Intercept)	1.957210	0.123145	1.23e-11 ***	0.2867
	larvae	0.004622	0.001610	0.0106 *	
$\sigma^{10\text{-}day}$ ~ blood spots	(Intercept)	2.00011	0.18847	6.43e-09 ***	0.0363
	blood spots	0.01399	0.01080	0.212	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

Table 6.1C: (Table 3.3.1 with other distributions and additional variables) The results from GLMs with different distribution that predicted flea (*Ceratophyllus vagabundus vagabundus*) larvae or adults that were collected in the first Barnacle goose (*Branta leucopsis*) nest samples (June 18, 2014) with the percent of goose eggs covered by blood in that nest (referred to as 'blood spots') and time as the predictor variables, and with the logarithm of the sample weights as an offset variable (*n*=20).

GLM (Poisson distribution)	Variable	Estimate	Std error	Pr(>|z|)	Dispersion parameter	AIC
larvae ~ blood spots, offset(log(sample weight))	(Intercept)	3.2.215005	0.042954	<2e-16 ***	114.657	1782.8
	blood spots	0.077281	0.001341	<2e-16 ***		
adult ~ blood spots, offset(log(sample weight))	(Intercept)	0.168006	0.207390	0.418	9.357066	202.7
	blood spots	0.077154	0.006477	<2e-16 ***		
GLM (Quasi-poisson)						
adult ~ blood spots, offset(log(sample weight))	(Intercept)	-0.50016	0.58520	0.40396	NA	NA
	blood spots	0.07379	0.02037	0.00194 **		
GLM (Negative Binomial)	**Variable**	**Estimate**	**Std error**	**Pr(>|z|)**	**Dispersion parameter**	**AIC**
larvae ~ blood spots + time, offset(log(sample weight))	(Intercept)	1.71074	0.97553	0.0795 .	1.146	255.82
	blood spots	0.09281	0.01899	1.02e-06 ***		
	time	0.04811	0.45540	0.4784		
adult ~ blood spots + time, offset(ln(sample weight))	(Intercept)	-2.52609	1.27120	0.0469 *	0.870	129.99
	blood spots	0.10797	0.02351	4.36e-06 ***		
	time	0.07879	0.06149	0.2000		

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

Table 6.1D: (Table 3.4 with additional variables)**:** The results from a GLMM with binomial distribution that predicted Barnacle goose (*Branta leucopsis*) egg hatching success with percentage of the egg covered by blood (referred to as 'blood spots'), hatch date and clutch size as predictor variables, and with nest as a random variable for all ringed geese nesting in the Storholmen colony (*n*=236, groups=73).

GLMM	Variable	Estimate	Std. Error	Pr(>|z|)	AIC
success ~ blood spots + hatch date + cutch + (1 | nest)	(Intercept)	3.96435	5.61303	0.48002	163.8
	blood spots	-0.29667	0.09830	0.00254 **	
	hatch date	-0.02606	0.25063	0.91719	
	clutch	1.35316	0.93044	0.14586	
success ~ blood spots + hatch date + (1 | nest)	(Intercept)	8.71690	4.66188	0.0615 .	164.1
	blood spots	-0.29883	0.09410	0.0015 **	
	hatch date	-0.01849	0.25266	0.9417	
success ~ blood spots + clutch + (1 | nest)	(Intercept)	3.40654	3.37008	0.31225	
	blood spots	-0.29521	0.09655	0.00223 **	161.9
	clutch	1.35699	0.93434	0.14640	
success ~ blood spots + (1 | nest)	(Intercept)	8.40343	1.78645	2.55e-06 ***	162.1
	blood spots	-0.29814	0.09352	0.00143 **	

Significance levels: .P<0.09, *P<0.05, **P<0.01, ***P<0.001

6.2 Photos

Figure 6.2A: Photo of blood spots on Barnacle goose (*Branta leucopsis*) eggs taken on June 18th, 2014. Blood spots appear on eggs after adult fleas feed excessively and defecate partially digested blood to feed their larvae (Askew 1971). This is the same nest as the one in Figure 6.2B (photo: Ross Wetherbee).

Figure 6.2B: Photo of blood spots on Barnacle goose (*Branta leucopsis*) eggs taken on June 26th, 2014. Blood spots appear on eggs after adult fleas feed excessively and defecate partially digested blood to feed their larvae (Askew 1971). Blood spots reduced in size during incubation, likely due to wear from incubating females. This is the same nest as the one in Figure 6.2A (photo: Ross Wetherbee).

Figure 6.2 C: Adult flea (*Ceratophyllus vagabundus vagabundus*) collected from a Barnacle goose (*Branta leucopsis*) nest in Kongsfjorden, Svalbard (photo: Ross Wetherbee).

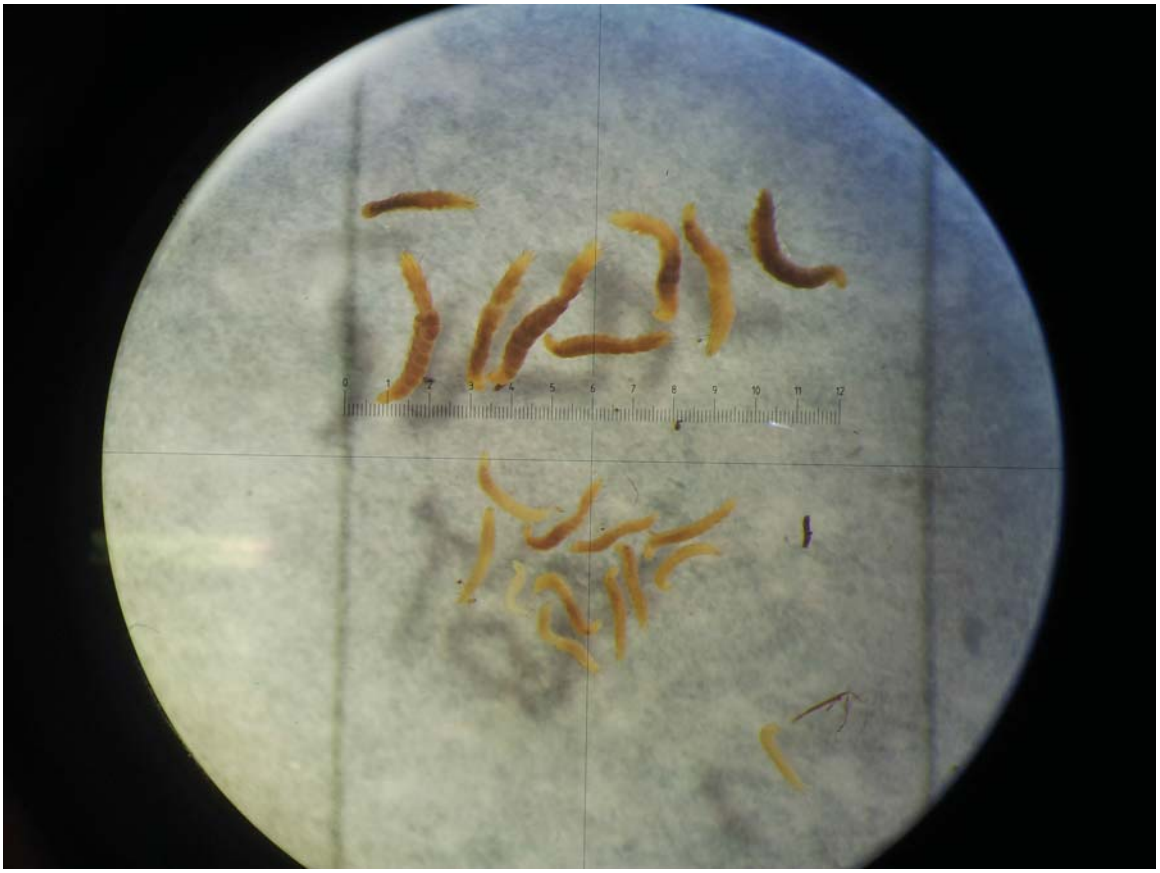


Figure 6.2 D: Two cohorts of flea larvae (*Ceratophyllus vagabundus vagabundus*) collected from the same Barnacle goose (*Branta leucopsis*) nest in Kongsfjorden, Svalbard. The cohorts were easily recognized in the samples due to their size difference. Larvae were classified as large when they were greater than 3mm and small when they were less than 3mm (photo: Ross Wetherbee).

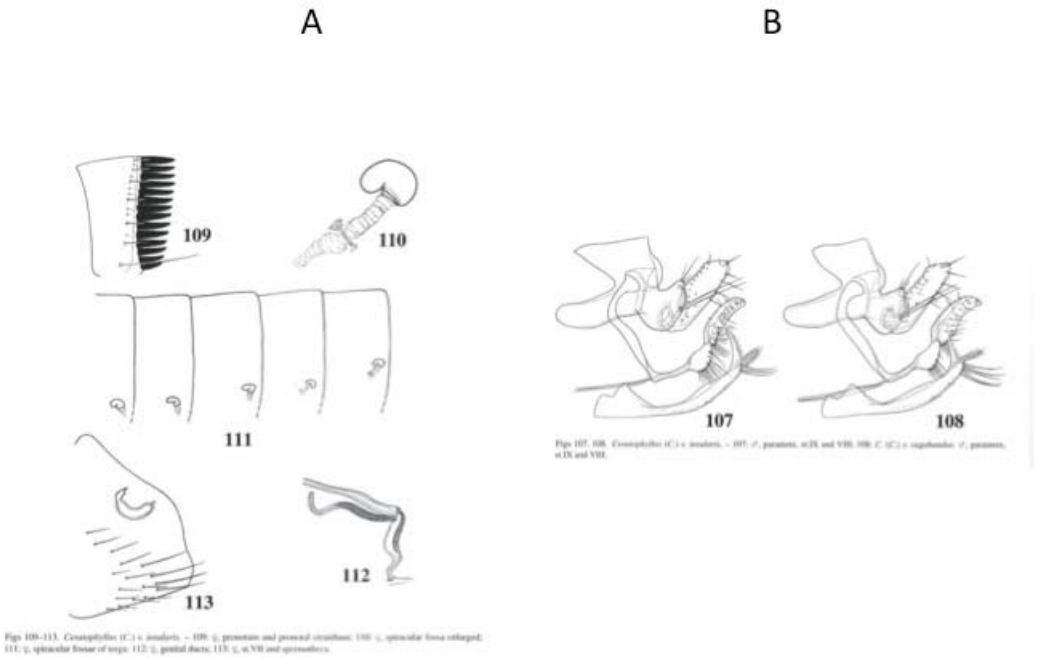


Figure 6.2 E: Diagnostic traits of the flea *Ceratophyllus vagabundus vagabundus*: 24 or more spines on the pronotum (all bird fleas), spines of pronotal ctenidium are much shorter then pronotum, strait posterior margin of sternum, spermatheca as in figure 113, genital ducts as in figure 112, as well as spiracular fossae of terga that is large with an elongated extension (Brinck-Lindroth & Smit 2007).

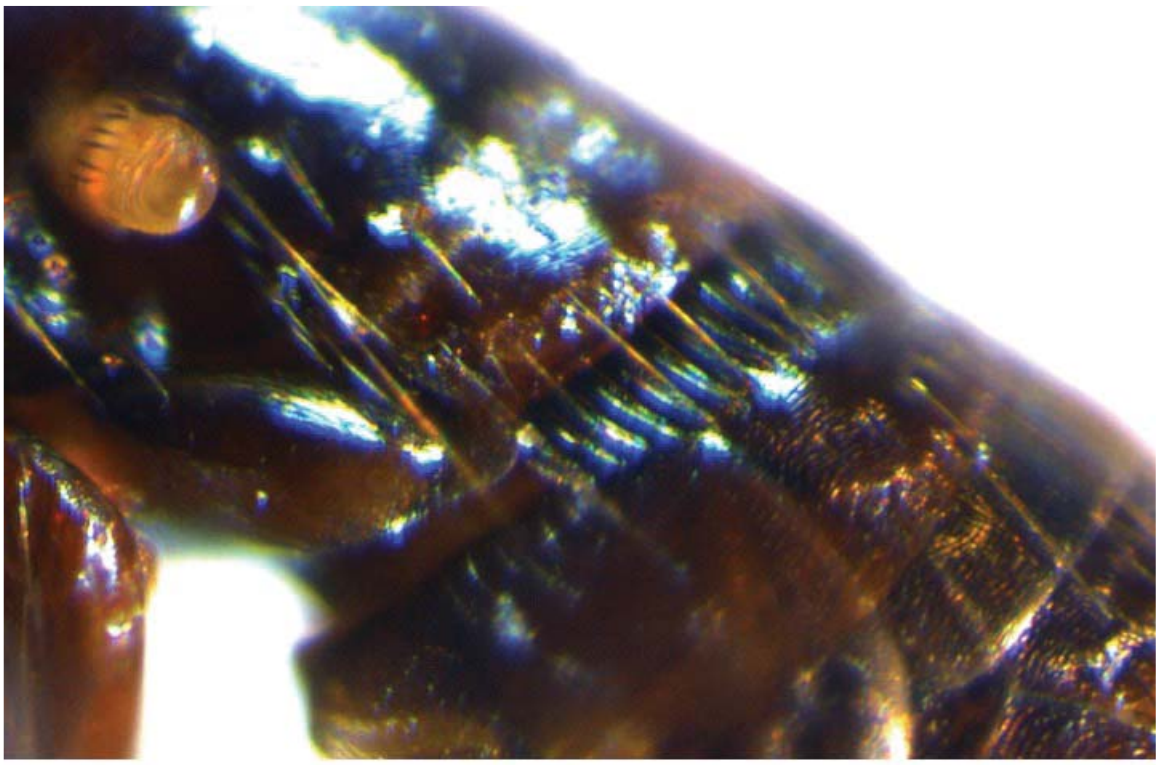
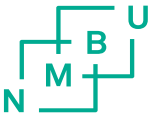


Figure 6.2 F: A photo of *Ceratophyllus vagabundus vagabundus* collected from a Barnacle goose (*Branta leucopsis*) nest in Kongsfjorden, Svalbard. *C. v. vagabundus* has 24 or more spines on the pronotum, and the spines of pronotal ctenidium are much shorter then pronotum (Brinck-Lindroth & Smit 2007, photo: Ross Wetherbee).

Figure 6.2 G: Photo a female Barnacle goose (*Branta leucopsis*) with a hatchling taken on Storholmen located in Kongsfjorden, Svalbard. Trap cameras were placed 2-4m from nests, and the photos were used to establish female goose recess time (photo: Ross Wetherbee).



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