Effects of Ectoparasite Burden on the Reproductive Success in Passerine Birds - Seasonal Effects of Feather Mite Migration on Blue Tits

Abstract

This work studies whether feather mites actively migrate along the wings of birds depending on season and weather conditions. We hypothesized that 1) feather mites would aggregate on the tertiary remiges of birds' wings during cold conditions; 2) feather mites would spread evenly over the entire wing during warm environmental conditions; and 3) that the teriaries of passerine birds are warmer or better insulated that the primaries or secondaries.

In winter 2010-2011 and in summer 2011 Blue Tits (*Cyanistes caeruleus*) were caught on "Schlammwiss", Uebersyren, Grand-Duchy of Luxembourg. The birds were captured using mist nets, banded, their morphometrics were recorded, and the exact number of feather mites (*Proctophyllodes stylifer*) per individual wing feather was noted. Thermal imaging was employed to measure the Blue Tits body temperature on different parts of their wings. The mean count of feather mites per feather type, i.e. primaries, secondaries, and teriaries were calculated. Kruskal-Wallis and Friedman tests were employed to back the hypotheses on feather mite migration. One-Way Analysis of Variance was used to determine significant differences between the different types of remiges on the Blue Tits' wings.

The findings revealed that *P.stylifer* in fact aggregates on tertiary remiges during cold environmental conditions. Moreover, *P.stylifer* not only spreads out over the entire remiges of Blue Tits during warm weather conditions, but statistical tests revealed that the feather mites prefer to aggregate on the primary remiges of the birds. Thermal imaging backs the hypothesis that tertiaries are indeed warmer or better insulated than the primary or secondary wing feathers.

We concluded that there was enough evidence to support the hypotheses, although the thermal imaging techniques may be improved for future studies.

Introduction

Animals, especially birds, particularly the relatively small species of the orders Apodiformes and Passeriformes, have major energy needs. It is common knowledge that songbirds and long-distance migratory birds are more energy-limited, than other birds (CIERLIK et al. 2004; PIERSMA 2002; PIERSMA et al. 1999). It is thus important that passerines, particularly small passerines, have to function with maximal energy efficiency, especially so during winter months at northern latitudes (>45° N). Suboptimal weather conditions, food bottlenecks, disease or parasites may cost the birds energy, which they don't have in excessive quantities.

All birds are thought to harbour some kind of parasite at some stage of their lives, either endo- or ectoparasites. Ectoparasites in European birds range in size from mites (Acarina), which are almost undetectable with the naked eye, through feather-lice (Mallophaga), fleas (Siphonaptera), to louse-flies (Hippoboscidae, also known as flat-flies), which are the size of a common housefly. All of these parasites feed on blood, feathers or skin of the passerine host (ROTHSCHILD and CLAY 1957). Some mite genera e.g. from the family *Pterolichidae* also feed on oil droplets from the bird's uropygial gland (DUBININ 1955) and others on fungi that grow within the bird's feathers, e.g. *Pterodectes rutilus* (Proctophyllodidae) and *Pteronyssoides nuntiaeveris* (Avenzoariidae) (BLANCO and TELLA 2001). Currently 2000 species in 33 families of feather mites are known (GAUD and ATEYEO 1996), however, Blue Tits in Europe are known to only have a single ectoparasite, namely *Proctophyllodes stylifer* (WILES et al. 2000).

Many bird species that have been found to be free of haemoparasites are highly infested with ectoparasites (MARTINEZ-ABRAIN et al. 2004). Eminent examples of this can be seen in the long-lived Procellariiformes and alpine swifts, which are highly infested with ectoparasites but apparently free of haemoparasites (GONZALEZSOLIS AND ABELLA 1997); (MERINO AND MINGUEZ 1998); (TELLA ET AL. 1998). Although ectoparasites can incur some cost to their host's fitness (MERINO ET AL. 1999), they do not cause death as some endoparasites do, especially haemoparasites, e.g. plasmodium. COX (2001) stated that under certain circumstances, ectoparasites may even have an overall positive effect on their hosts – thus they would not be parasites *per se* anymore.

From an evolutionary perspective, research suggests that many bird species, especially birds of prey (e.g. Falconiformes), but also several species of songbirds for example the European Starling (*Sturnus vulgaris*) that re-use their nests from year to year, have evolved 'medical skills'. They use green plants to fumigate their nests with insect repelling qualities or even insecticidal compounds to tackle ectoparasite burden (WIMBERGER 1984) or to ward off endoparasite vectors, e.g. *Culex quinquefasciatus* as vector for avian malaria (LEVIN et al. 2009).

Furthermore, Eastern Screech-Owls (*Megascops asio*) bring live blind snakes (*Leptotyphlops dulcis*) to their nestlings, whereas all other prey is delivered dead. Some of the snakes are eaten, but most remain unharmed in the nest debris, where they feed on insect larvae. Consumption of the larvae may reduce larval parasitism. Nestlings in nests containing a snake grow faster and their mortality rate is reduced. GEHLBACH AND BALDRIDGE (1987) suggest a commensal relationship in which the Screech-Owl benefits reproductively and the blind snake remains unharmed.

So far, observations of successful adaptations to combat parasitism in European songbirds have not been widely documented. MENNERAT *et al.* (2008) hypothesised, that aromatic plants brought to the nests by blue tits (*Cyanistes caeruleus*) on Corsica would have anti-blow fly qualities during the chick-rearing stage, but no significant relation was found between amount of aromatic plants in nests and blow fly infestation intensity.

On one hand, these findings raise the question as to whether ectoparasites in European passerines affect their host at all: Food may be so abundant and/or our temperate climate may be so mild, that the birds have no difficulty in coping with parasite burden. On the other hand, why would Screech-Owls, European Starlings, and other species go through all the trouble involved in bringing live prey to their nests or fumigating their nests, etc., seemingly without any benefit to their survival? The research of many great minds, including KARELL et al. (2011), RICHNER et al. (1993), MERINO AND POTTI (1995), and MOLLER (1990), leads to the conclusion that these behavioural traits must be beneficial to the species survival.

As, until now, the basics have not been covered in many aspects, this work is not going to directly investigate the impact of parasite burden on the reproductive fitness of the host. This project will investigate the seasonal behaviour of *P. stylifer*, especially *P. stylifer*'s migration on the Blue Tit (*Cyanistes caeruleus*) host. However, *P. stylifer* is merely a model organism in this case, as no negative parasitic behaviour has been observed of the species. *P. stylifer* is a commensal organism, which is the only species of feather mites that occurs on the wings of Blue Tits according to ATYEO and BRAASCH (1966). *P. stylifer* lives all its developemental stages, i.e. egg, larva, protonymph, tritonymph and adult, within the plumage of the same host. The usual sites where *P. stylifer* is encountered are the remiges and the rectrices of the bird where they can be found tandemly positioned between the barbs of the rachis [Fig.1] (ATYEO and BRAASCH 1966). It is presumed here that similar behaviour would be true for other, more harmful, parasitic feather mites too.

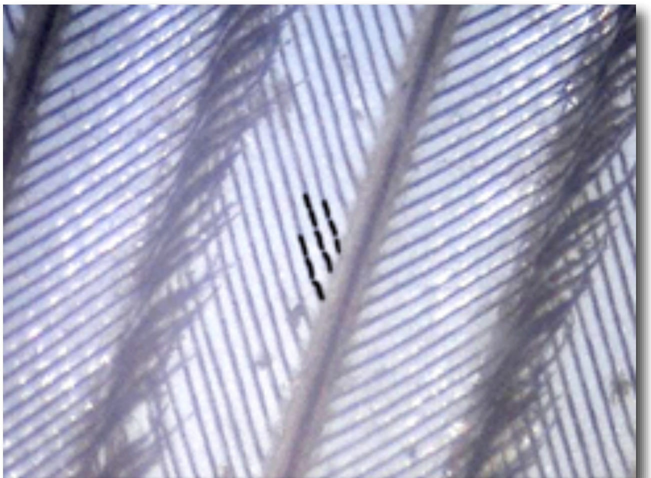

Fig.1: Graphical approximation of feather mites' positioning on wing feather. There would be 10 mites in this example.

Hypotheses

1) During cold weather conditions *P. stylifer* will accumulate on the tertiary wing feathers.

2) During warm weather conditions *P. stylifer* will spread evenly over the entire wing feathers.

3) Tertiary wing feathers are warmer or better insulated than the primary and secondary wing feathers.

Materials & Methods

Study site and capture of birds

The work presented here was carried out on "Schlammwiss", Uebersyren, Grand-Duchy of Luxembourg (Lat 49.6385°; Lon 6.2755°; mean altitude: 250 mNN). "Schlammwiss" is a 375 ha NATURA 2000, Birds Directive Site (SPA – LU0002006) with 21 protected bird species. "Schlammwiss" includes the following habitat classes:

- Inland water bodies (0.3%)
- Bogs, Marshes, Water fringed vegetation, Fens (4.5%)
- Heath, Scrub, Maquis and Garrigue, Phygrana (1.4%)
- Humid grassland, Mesophile grassland (0.7%)
- Improved grassland (65.5%)
- Other arable land (17.5%)
- Broad-leaved deciduous woodland (7.3%)
- Coniferous woodland (0.1%)
- Artificial forest monoculture (0.1%)
- Orchard (0.3%)
- Other land (2.3%)

Bird capture itself however occurred within 150 ha of the site, including the habitats:

- Inland water bodies (on river Syre and several ponds)
- Water fringed vegetation (reed beds)

- Scrub
- Humid grassland
- Improved grassland
- Deciduous woodland
- Orchard

Birds were caught using mist nets (Height: 3 m; Mesh size: 15 mm) and handled in accordance with established procedures of the Luxembourgian Trust for the Protection of Birds and the Environment (LNVL) by trained bird ringers. Birds were attracted using sound lures and in winter additional feeding occurred through feeding stations baited with sunflower and other seeds. Well within 30 minutes of capture the birds were banded and their morphometric measurements were recorded, including species, age, sex (when possible), wing length, body mass, fat deposits (KAISER 1993), and muscles.

Capture occurred in December 2010 and January 2011 for the winter data collection and during June, July, and August 2011 for the Summer data collection. Temperature and other meteorological data was obtained from the meteorological service on Findel airport, which is located 2.7 km from "Schlammwiss"

Mite count

After the standard recordings (see above) the right wing of the bird was extended and held to ambient light. Mites were then counted by eye, starting at the first (outermost) primary feather and working along the wing to the last (innermost) tertiary feather. If coverts were in the way they were gently moved aside to expose the entire feather. If the right wing was completely free of mites, the procedure was repeated for the left wing, although in general the feather mite burden was not significantly different among the two wings. Feather mites were visible along the shaft, the barbs, and the barbules of feathers [Fig.1]. Mite counts were recorded in exact numbers, together with the birds' relative ring number, presciently for future studies where mite occurrence may be examined relative to morphometric data as shown for example in SCHMIT (2010). The mite counting and recording took approximately five minutes per bird. [**Annexe 1**]

Infra-Red imaging

To test whether the tertiary remiges are better insulated/warmer than the primaries or secondaries, infra-red imaging was used. The IR camera was the FLIR® i60. It is a lightweight professional IR camera with an integrated high quality visual digital camera (2.3 MPx). The FLIR® i60 has a field of view of α = 25°, its minimum focus distance however is >0.6 m (although the technical specs provided by the manufacturer indicate 0.1 m). The thermal sensitivity of FLIR® i60 is 0.1°C with a thermal range between -20°C to +120°C, and the IR resolution is 32.4 KPx (0.0324 MPx or 180 x 180 Px) [**Annexe 2**].

After the feather mites were counted, IR images were taken from 35 *C. caeruleus*. Unfortunately pictures were only taken during the summer months, as the camera wasn't available in winter yet. The IR images were evaluated with an emissivity of 0.95 (WARD et al. 2007; WARD et al. 1999), atmospheric temperature and relative air humidity were obtained from the Luxembourgian Aerial Navigation Administration. The IR pictures were enhanced and evaluated using "FLIR® Quick Report" software as well as "ADOBE® Photoshop Creative Suite 5®". Point measurements were taken from the respective centres from each type of remiges from six IR images taken at different times of day.

Data processing

The recorded data were entered into a Microsoft® Excell® Spreadsheet. Mite numbers for primary (p1-p10), secondary (s1-s6), and tertiary (t1-t3) remiges were then added to give the total mite count per individual bird's primary, secondary and tertiary remiges respectively.

Next, the means for each feather type were calculated for each specimen, and the non-parametric Kruskal-Wallis test was carried out for statistical analysis to check for significant differences using Minitab 15 software. A non-parametric test was used as opposed to ANOVA, because the data wasn't normally distributed, and the data didn't have equal variances.

R statistical software was used to conduct the Friedman test where the actual feather mite counts were employed, i.e. not the means of all feathers within each feather type. This test was used if the data was not independent, which remains unclear.

One-Way ANoVA was carried out, using R software, to determine whether the temperature difference for the three types of remiges was significant. For this analysis six thermal images of different birds at different times of day during summer were used.

Results

Winter mite counts

Minitab 15 output:

Kruskal-Wallis Test: Values vs Mean Winter Remiges

```
Kruskal-Wallis Test on Values

Mean Win Remiges    N  Median  Ave Rank      Z
Mean Win Prim      48  0.2000      54.7  -3.62
Mean Win Sec       48  0.9167      76.6   0.83
Mean Win Tert      48  2.3333      86.2   2.79
Overall           144              72.5

H = 14.39  DF = 2  P = 0.001

H = 14.65  DF = 2  P = 0.001  (adjusted for ties)
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The P-value of 0.001 shows high significant differences within the data set. The median for tertiaries being much higher than for primaries and secondaries shows that the tertiaries have the highest mite count [see also

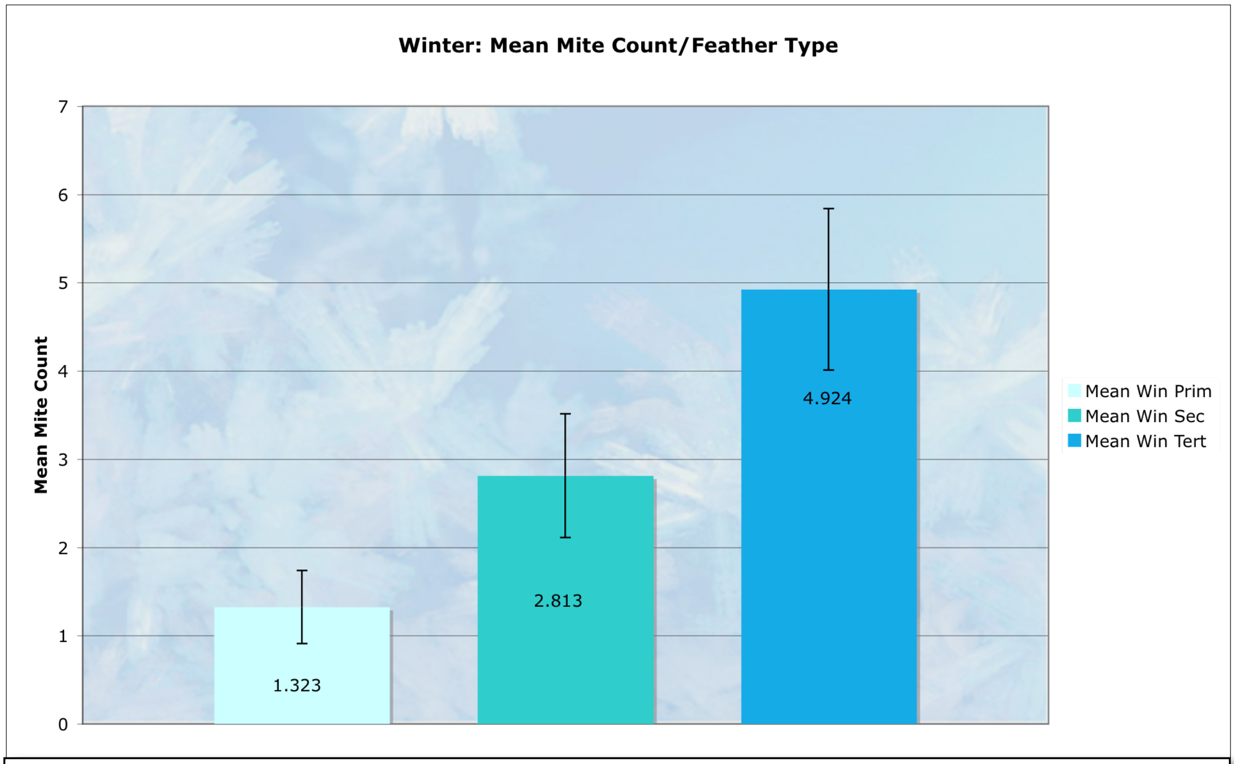

Fig.2: Histogram showing average mite counts per feather type for individual remiges in winter with standard error bars.

Friedman Test: Values vs Winter Remiges

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Friedman Test on Values: Friedman X² = 8.9816, DF = 2, p-value = 0.011
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Summer mite counts

Minitab 15 output:

Kruskal-Wallis Test: Value versus Mean Sum Remiges

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Kruskal-Wallis Test on Value

Mean Sum Remiges     N       Median  Ave Rank      Z
Mean Sum Prim       43  0.400000000      83.6   4.00
Mean Sum Sec        43  0.166666667      63.8  -0.25
Mean Sum Tert       43  0.000000000      47.5  -3.75
Overall            129                   65.0

H = 20.12  DF = 2  P = 0.000
H = 22.16  DF = 2  P = 0.000  (adjusted for ties)
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The P-value of 0.000 shows high significant differences within the data set. The median for primaries being much higher than for secondaries and tertiaries shows that the primaries had the highest mite count [see also **Figure 3**].

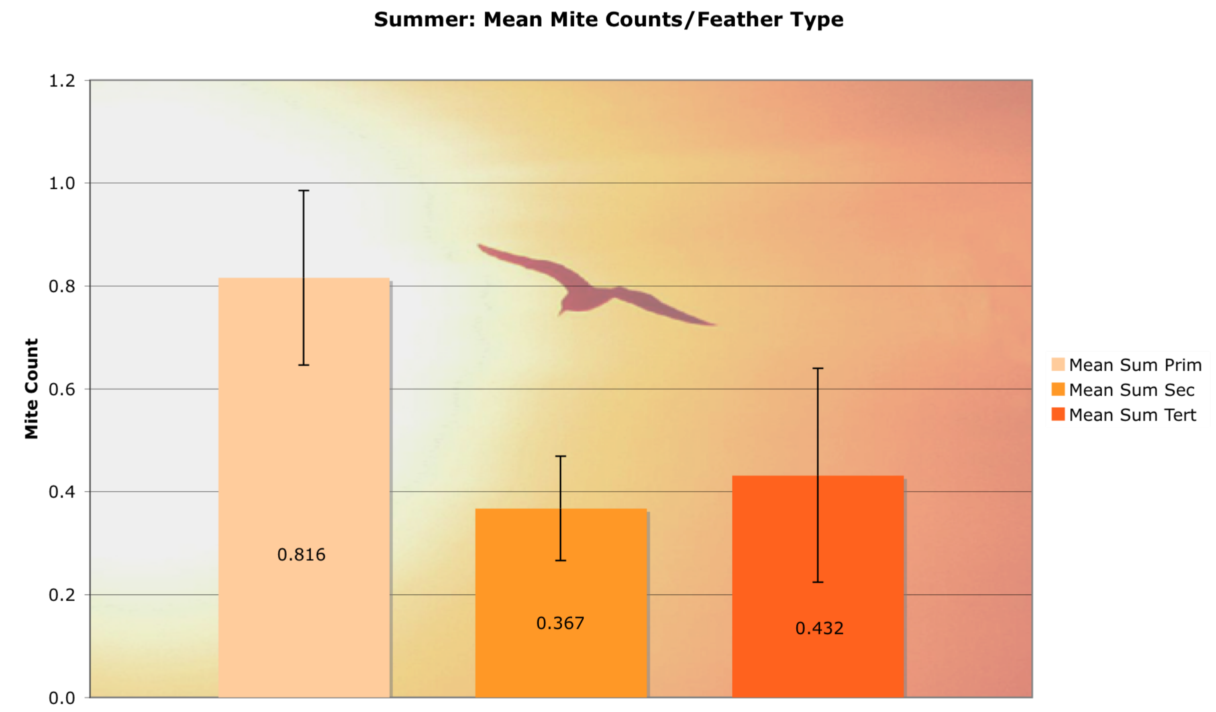

Fig.3: Histogram showing average mite counts per feather type for individual remiges in summer with standard error bars.

Friedman Test: Values vs Summer Remiges

Friedman Test on Values: Friedman X^2 = 47.3284, DF = 2, p-value = <0.001

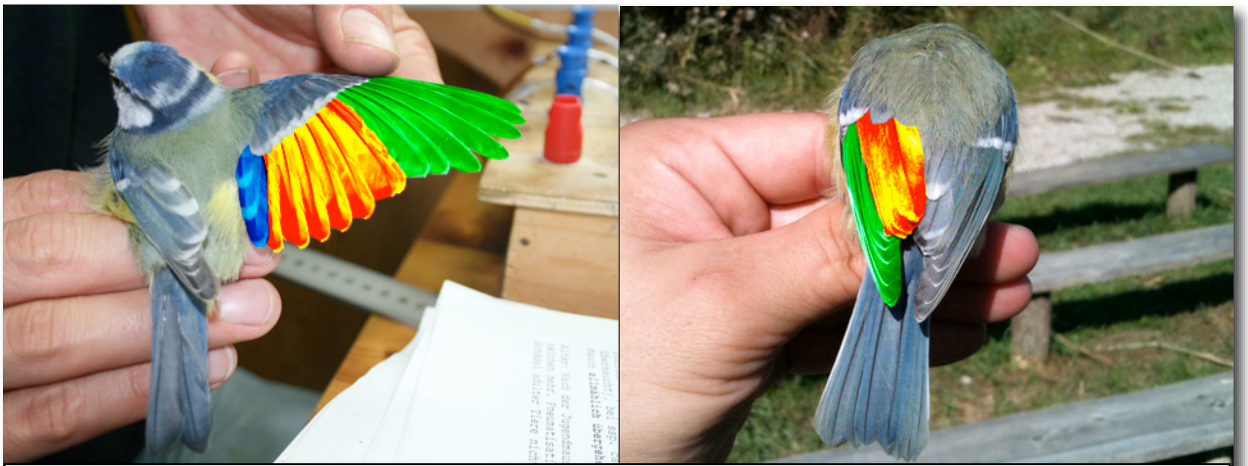

Fig.4: *C.caeruleus* with wing spread out (left) and sitting (right). The primaries (green), the secondaries (orange), and the tertiaries (blue) were highlighted for visualisation. On the sitting bird, the tertiaries are completely covered by the other remiges.

Feather Temperatures

Visual observations on *C.caeruleus* revealed that the tertiary remiges on the sitting bird are covered by the primary and secondary remiges, hence they are better insulated [see **Figure 4**].

Moreover, downy feathers on *C.caeruleus*' neck completely cover the location of the tertiaries on the sitting bird. Infrared imaging revealed that the tertiary remiges are on average 2.48°C warmer than secondary remiges and 4.17°C warmer than the primaries [**Figure 5**]. One-Way ANoVA, which was carried out, using R software, generated the following output:

```
> anova(fit)
Analysis of Variance Table

Response: Temperature
                    Df     Sum Sq    Mean Sq    F value     Pr(>F)

     Class          1      52.083    52.083     7.686       0.01359 *

     Residuals      16     108.422   6.776
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The P-value of 0.014 (95% confidence level) indicates a significant difference in temperature between the three types of remiges.

Evaluation of the Results

The statistical tests that were carried out clearly back the hypothesis that in winter *P.stylifer* aggregate on the tertiary remiges of *C.caeruleus*' wings. Moreover, in summer *P.stylifer* not only spread out over the entire wing, but they prefer to aggregate on the primaries of the birds. The Friedman Test also shows a significant difference as the critical value for Chi-squared at 2 degrees of freedom is at 5.991 and Chi-squared clearly

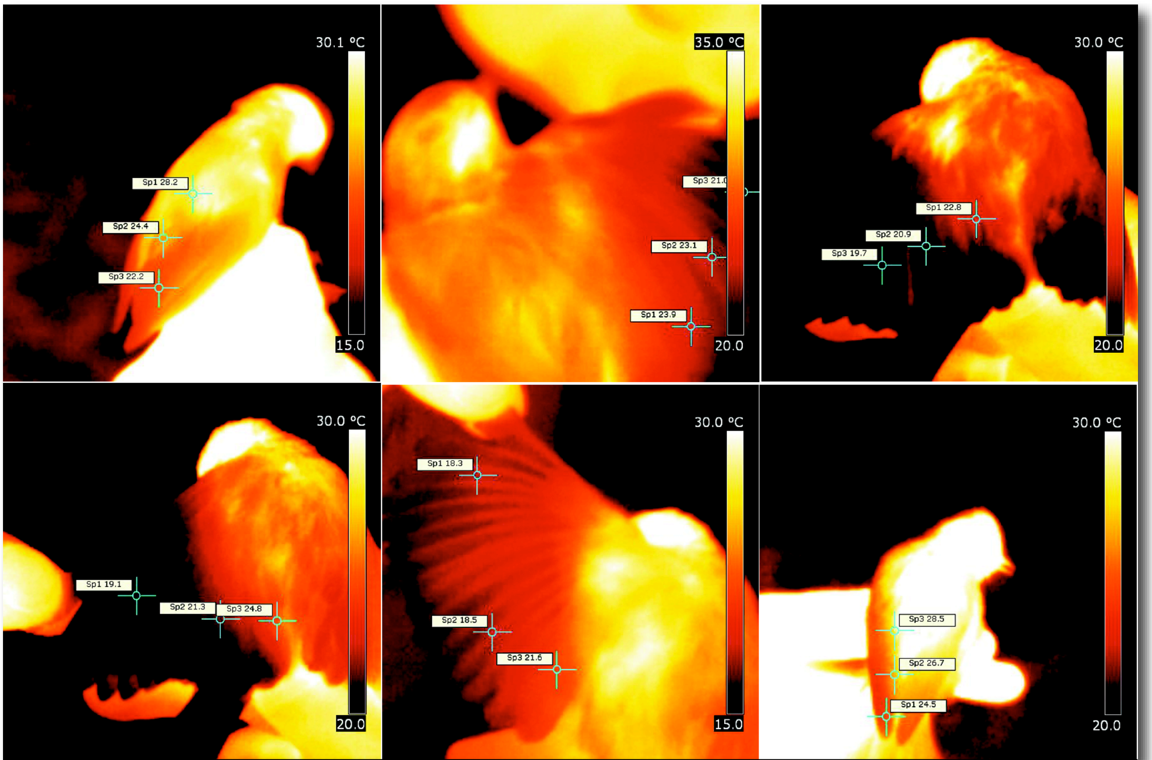

Fig.5: Infrared images of six different birds at different times of day. Pinpoint measurements in °C were obtained using FLIR® Quick Report® software.

exceeds the critical value for both winter and summer. The infrared images confirm that, at least in summer, the tertiary remiges are warmer than the primaries or secondaries.

Discussion

Possible Error sources

Due to breeding seasons, and possibly other ecological factors, only adult birds were caught in winter and only juvenile birds were caught in summer. These age differences may account for some of the observed patterns, such as that there were significantly more feather mites present on the birds' wings in winter (i.e. adults) as there were during summer (i.e. juveniles). A possible explanation for these observations is that older birds have had more time already to become infested with feather mites. On the other hand it is know that moulting occurs at different times for adults and juvenile Blue Tits respectively. Juvenile Blue Tits moult for the first time from the beginning of July onwards (SVENSSON 2006). Data collection for summer started at the end of July, hence most of the juvenile Blue Tits that figure in the data collection had already undergone the first moult and may therefore have shed the mites together with their plumage. The adult birds that were caught in winter however undergo complete moult after their breeding season (SVENSSON 2006), thus their plumage was more than six months old by the time the mites were counted, hence mites have had more time to accumulate. Although JOVANI AND SERRANO (2001) postulate that feather mites of the suborder Astigmata avoid moulting feathers by migrating in front of the moulting sequence.

A factor to consider is that birds experience a great deal of stress during capture and handling (CALISI et al. 2008; NEWMAN et al. 2005; SORACE et al. 2001). As a result of varying stress levels the levels of blood flow directed to the wings and possible muscular contractions the measured temperatures may be affected.

Infrared imaging was only used in summer, because the equipment wasn't available at the time of the winter measurements. There is a good chance that the findings may have been different either way. For example, it is possible that the temperature differences would have been greater in winter, which would indicate that the tertiary remiges would be better insulated. On the other hand, it is possible that the differences in temperature for the three feather types would have been smaller, which could indicate that insulation is not such an important factor after all and there may have been another explanation why *P.stylifer* aggregates on the tertiary feathers. Moreover, the infrared contrast between the background and the bird itself would have been much greater in winter, due to lower background temperatures, and it would have been easier to focus the IR camera on the study objects, giving more accurate thermal data.

It was not possible to use the correct emissivity particularly for blue tits, as the only emissivities found in literature were those of brown-grey Canada Geese and European Starlings (AVILES et al. 2010; BEST and FOWLER 1981). Starlings reflect a great deal into the ultraviolet spectrum (BENNETT et al. 1997), but that is the other side of infrared part of the electromagnetic spectrum and could therefore be ignored. However, the thermal evaluation in FLIR® Quick Report was conducted with emissivities from 0.90 to 1.00 and the differences in temperature readings were negligible as they varied by less than 0.005 °C. Perhaps another model of thermal camera would have been able to pick out these subtle differences more accurately.

Another problem was that the specifications of the FLIR® i60®, which indicated that it had a minimal distance to the study object of 50 cm, however experiences in the field were different. The distance needed to be at least 70 cm to achieve appropriate focus, but no more than 100 cm or the small birds would no longer take up the main portion of the image. Different equipment, such as the FLIR® T425® [**Annexe 3**], would have been more up to the task with its interchangeable optics, its smaller focal length, and its higher IR resolution. Using the given equipment, two people needed to take the infrared images in tandem, i.e. one held the bird and the other one the camera. The named drawbacks were severely limiting to the experimental possibilities for this work. Furthermore, within the collection of 35 birds' IR images that were taken for this work, only a few could be used to back the hypothesis. In part because of the problems mentioned in this paragraph, but as well because the infrared radiation of the fingers of the person that held the birds for the camera often penetrated the feathers of the subjects, rendering the pictures unusable for thermal measurements. Different bird handling procedures here would benefit future experiments of this nature.

The thermal evaluation possibilities were limited by the FLIR® Quick Report software. Quick Report doesn't allow average measurements over a specific area of the image; it only allows point measurements. It was therefore a slightly subjective test as it was up to the researcher to determine which point to include in the statistical analysis. The measurements were however pinpointed using an educated guess on what point would represent an overall average value.

For the statistical tests that were carried out for this work, one could argue that the Kruskal-Wallis test was not appropriate. Although Kruskal-Wallis (KW) is a non-parametric equivalent to the Analysis of Variance (ANOVA), KW assumes independent observations. In this work however, multiple measurements were taken of three different feather types, but from the same bird for each sample. The Friedman test may have been the better choice, as it does not assume independent variables, however, Minitab 15® software doesn't include any post-hoc test that allow to verify which variables are different from each other. Since the P-value was significant for Kruskal-Wallis as well as for Friedman, Friedman was employed to carry out the correct test and Kruskal-Wallis was employed to observe the medians of the three types of feathers to deduct where the actual differences lie.

Suggestions for Further Study

In my opinion the biggest problem with this study was the ratio between adults and juveniles for winter and summer respectively. As mentioned above, during summer fieldwork only juvenile Blue Tits were caught and examined and during winter fieldwork only adult birds were captured and examined. The results later showed much greater numbers of mites on winter birds compared to mite numbers on summer birds. For this reason it is difficult to arrive at a definite conclusion as not enough facts are known about the ecology of *P.stylifer* or other feather mites. These findings may have been the result of *P.stylifer*'s life cycle, but it is just as well possible that these findings were the result of young birds not having had enough time to accumulate these high parasite numbers. In addition, the temperature distribution across the wing may be different for juveniles. This may be the factor that caused equal distribution, and it may have nothing to do with summer or winter. The differing parasite numbers of adult or juvenile Blue Tits could be any of the named reasons or any other result of ecological interactions or environmental factors. These conclusions suggest that more research can be carried out, both by means of capturing a more homogeneous sample set and on the ecological relationships between *P.stylifer* and *C.caeruleus* or even the life cycles of parasitizing feather mites themselves.

Another suggestion for further study is the use of different IR imaging equipment as I'm convinced that much more accurate and meaningful thermal data could have been obtained. For the next study the thermal camera used should be able to function at a shorter distance from the study object (i.e. shorter focal range) as well as at a higher infrared resolution.

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References

ATYEO, WARREN T., and BRAASCH, NORMAN L. (1966). "The feather mite genus Proctophyllodes (Sarcoptiformes: Proctophyllodidae)." *Univ Nebr State Mus Bull*, 5, 1-351.

AVILES, JESUS M., PAREJO, DESEADA, PEREZ-CONTRERAS, TOMAS, NAVARRO, CARLOS, and SOLER, JUAN J. (2010). "Do spotless starlings place feathers at their nests by ultraviolet color?" *Naturwissenschaften*, 97(2), 181-6.

BENNETT, A. T. D., CUTHILL, I. C., PARTRIDGE, J. C., and LUNAU, K. (1997). "Ultraviolet plumage colors predict mate preferences in starlings." *Proceedings of the National Academy of Sciences of the United States of America*, 94(16), 8618-8621.

BEST, R. G., and FOWLER, R. (1981). "Infrared Emissivity and Radiant Surface Temperatures of Canada and Snow Geese." *Journal of Wildlife Management*, 45(4), 4.

BLANCO, G., and TELLA, J. L. (2001). "Feather mites on birds: costs of parasitism or conditional outcomes?" *Journal of Avian Biology*, 32(3), 271-274.

CALISI, REBECCA M., RIZZO, NORMA O., and BENTLEY, GEORGE E. (2008). "Seasonal differences in hypothalamic EGR-1 and GnIH expression following capture-handling stress in house sparrows (Passer domesticus)." *General and Comparative Endocrinology*, 157(3), 283-287.

CIERLIK, G., TWOREK, S., MAKOMASKA-JUCHIEWICZ, M., and PROFUS, P. (2004). "Metabolic rates in passerine birds: Effects of adaptive strategies and taxonomy." *Ekol. Bratisl.*, 23(2), 207-224.

COX, F. E. G. (2001). "Concomitant infections, parasites and immune responses." *Parasitology*, 122, S23-S38.

DUBININ, V. B. (1955). "New genera and species of feather mites Referat. Zhur., Biol., 1956, No. 73148. (Translation.)." *Trudy Zool Inst Akad Nauk Sssr*, 1955((18)), 248-287.

GAUD, J., and ATEYEO, W.T. (1996). "Feather mites of the world (Acarina, Astigmata): the supraspecific taxa. Part I." *Annalen Zoologische Wetenschappen*(277), 193.

GEHLBACH, F. R., and BALDRIDGE, R. S. (1987). "Live Blind Snakes (*Leptotyphlops dulcis*) in Eastern Screech-Owl (*Otus asio*) Nests - A Novel Commensalism." *Oecologia*, 71(4), 560-563.

GONZALEZSOLIS, J., and ABELLA, J. C. (1997). "Negative record of haematozoan parasites on Cory's Shearwater *Calonectris diomedea*." *Ornis Fennica*, 74(3), 153-155.

JOVANI, R., and SERRANO, D. (2001). "Feather mites (Astigmata) avoid moulting wing feathers of passerine birds." *Animal Behaviour*, 62, 723-727.

KAISER, A. (1993). "A New Multi-Category Classification of Subcutaneous Fat Deposits of Songbirds." *J. Field Ornithol.*, 64(2), 246-255.

KARELL, P., AHOLA, K., KARSTINEN, T., KOLUNEN, H., SIITARI, H., and BROMMER, J. E. (2011). "Blood parasites mediate morph-specific maintenance costs in a colour polymorphic wild bird." *Journal of Evolutionary Biology*, 24(8), 1783-1792.

LEVIN, IRIS I., OUTLAW, DIANA C., HERNAN VARGAS, F., and PARKER, PATRICIA G. (2009). "Plasmodium blood parasite found in endangered Galapagos penguins (*Spheniscus mendiculus*)." *Biological Conservation*, 142(12), 3191-3195.

MARTINEZ-ABRAIN, A., ESPARZA, B., and ORO, D. (2004). "Lack of blood parasites in bird species: Does absence of blood parasite vectors explain it all?" *Ardeola*, 51(1), 225-232.

MENNERAT, A., PERRET, P., CARO, S. P., HEEB, P., and LAMBRECHTS, M. M. (2008). "Aromatic plants in blue tit *Cyanistes caeruleus* nests: no negative effect on blood-sucking *Protocalliphora* blow fly larvae." *Journal of Avian Biology*, 39(2), 127-132.

MERINO, S., and MINGUEZ, E. (1998). "Absence of haematozoa in a breeding colony of the storm petrel *Hydrobates pelagicus*." *Ibis*, 140(1), 180-181.

MERINO, S., MINGUEZ, E., and BELLIURE, B. (1999). "Ectoparasite effects on nestling European Storm-petrels." *Waterbirds*, 22(2), 297-301.

MERINO, S., and POTTI, J. (1995). "Mites and Blowflies Decrease Growth and Survival in Nestling Pied Flycatchers." *Oikos*, 73(1), 95-103.

MOLLER, A. P. (1990). "Effects of a Hematophagous Mite on the Barn Swallow (*Hirundo rustica*) - A Test of the Hamilton and Zuk Hypothesis." *Evolution*, 44(4), 771-784.

NEWMAN, SCOTT H., CARTER, HARRY R., WHITWORTH, DARRELL L., and ZINKL, JOSEPH G. (2005). "Health assessments and stress response of Xantus's Murrelets to capture, handling and radio-marking." *Marine Ornithology*, 33(2), 147-154.

PIERSMA, T. (2002). "Energetic Bottlenecks and other Design Constraints in Avian Annual Cycles." *Integrative and Comparative Biology*, 42(1), 51-67.

PIERSMA, T., GUDMUNDSSON, G. A., and LILLIENDAHL, K. (1999). "Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird." *Physiological and Biochemical Zoology*, 72(4), 405-415.

RICHNER, H., OPPLIGER, A., and CHRISTE, P. (1993). "Effect of an Ectoparasite on Reproduction in Great Tits." *Journal of Animal Ecology*, 62(4), 703-710.

ROTHSCHILD, MIRIAM, and CLAY, THERESA. (1957). *The New Naturalist - Fleas, flukes and cuckoos. A study of bird parasites*: Macmillan Co.

SCHMIT, X. M. P. (2010). *The Effects of Ectoparasite Burden on the Physiology of Passerine Birds*, Final Year Project, Cardiff University, Cardiff.

SORACE, A., GUSTIN, M., and LANDUCCI, G. (2001). "Evening mist-net closure: Implications for data collection and bird welfare." *Ringing and Migration*, 20(4), 371-376.

SVENSSON, L. (2006). *Identification Guide to European Passerines*, Norfolk: British Trust for Ornithology.

TELLA, J. L., GAJON, A., GORTAZAR, C., and OSACAR, J. J. (1998). "High host specificity of Crataerina melbae (Diptera: Hippoboscidae) in a mixed colony of birds." *Journal of Parasitology*, 84(1), 198-200.

WARD, JENNIFER M. ;, MCCAFFERTY, DOMINIC J. ;, RUXTON, GRAEME D. ;, and HOUSTON, DAVID C. (2007). "Thermal Consequences of Turning White in Winter: A Comparative Study of Red Grouse *Lagopus lagopus scoticus* and Scandinavian Willow Grouse *Lagopus lagopus lagopus*." *Wildlife Biology*, 13(2), 10.

WARD, S., RAYNER, J. M., MOLLER, U., JACKSON, D. M., NACHTIGALL, W., and SPEAKMAN, J. R. (1999). "Heat Transfer from Starlings *Sturnus vulgaris* during Flight." *J. Exp. Biol.*, 202(12), 9.

WILES, P. R., CAMERON, J., BEHNKE, J. M., HARTLEY, I. R., GILBERT, F. S., and MCGREGOR, P. K. (2000). "Season and ambient air temperature influence the distribution of mites (Proctophyllodes stylifer) across the wings of blue tits (Parus caeruleus)." *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 78(8), 1397-1407.

WIMBERGER, P. H. (1984). "The Use of Green Plant-Material in Bird Nests to Avoid Ectoparasites." *Auk*, 101(3), 615-618.