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Effects of weather conditions on the reproductive success of House Sparrows

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Budapest

2012

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Introduction

The effects of environmental circumstances on various behaviors of animals have often been documented, and nowadays studies on the effects of climatic factors are getting more attention. The global average temperature is increasing on the Earth, and this process was getting faster in the last 50 years (Parmesan 2006). There are scenarios also for the Pannonian Basin based on regional climate modeling. These models have predicted increasing average temperature, mostly in summer, and more heat waves. They have also predicted decreasing precipitation per year, principally in summer, but more precipitation in winter. The length of droughts and frequency of strong rainfalls may increase in the area of Hungary (Faragó, Láng & Csete 2010).

The effects of weather on behavioral traits have been studied mostly for avian migration, e.g. the timing and the route of the migration (Lusk, Guthery & Demaso 2001; Sinelschikova *et al.* 2007; Gordo 2007) and other phenological changes such as the timing of breeding in animals (Dawson 2008; Ardia & Cooper 2006). Recently, several studies documented that the timing of avian migration and yearly reproductive attempts were shifted earlier (Gordo 2007). Moreover, the species' range, habitat, demographical and morphological traits can also change in response to climate warming (Crick 2004; Yom-tov *et al.* 2006; Kovács *et al.* 2010; Lavergne *et al.* 2010). The degree of the adaptation of the species to the altering climate depends on several ecological and life-history characteristics (Végvári *et al.* 2010). Migration, breeding and predation are time-sensitive phenological processes, and mismatches of these processes can alter the rates of reproduction and survival, causing decline in some populations and increase in others (Miller-Rushing *et al.* 2010). Møller, Rubolini & Lehikoinen (2008) have found in a comparative study that bird species which cannot respond to recent climate change by shifting their spring migration phenology have declining breeding populations, whereas species which advanced their migration phenology have stable or increasing populations in Europe.

Thus, climate change may have crucial fitness consequences in animal populations. Knowledge about the effects of weather on the biota is important for understanding the past and future effects of the climate change. Because climate change models predict an increase both in the average temperature and in the frequency of extremities such as heat waves, droughts and heavy rainfall, studying how these local weather conditions influence the fitness of animals can help to predict their future effects. Extreme climatic events are little studied,

probably because they are rare, but this lack of studies can be problematic because we know very little about the ability of animals to adapt to such extreme situations (Møller 2011). Therefore, beyond the long term phenological monitoring of populations (Crick & Sparks 2006; Csörgő, Harnos & Kovács 2009), reproductive behaviour and fitness of individuals should be examined in connection with weather variability to understand how meteorological events get "translated" into responses at the population or individual level. Although weather conditions are often included into fitness studies as a disturbing or background factor (Ardia & Cooper 2006; Londoño, Levey & Robinson 2008, Peach *et al.* 2008; Chastel & Kersten 2002), the effects of weather *per se* on animal populations has been less studied up to now (Dawson, Lawrie & O'Brien 2005; Lifjeld, Dunn & Whittingham 2002), especially those beyond the gross effects average temperature and precipitation, such as the variability and extremity of weather conditions.

Fitness in birds is estimated most often by hatching success of clutches and number of nestlings fledged. Besides these proxies, sex ratio of the offspring can also be a component of reproductive success, because the long-term survival and reproductive prospects of male and female offspring may be different. Extreme or unfavorable weather may affect sons and daughters differently during their ontogeny, but this phenomenon is yet little documented (Weatherhead 2005; Torres & Drummond 1999).

In this study, I have examined the reproductive success in a House Sparrow (*Passer domesticus*, Linnaeus, 1758) population in Hungary, in relation to local weather conditions and the variability of local weather to understand the effects of weather and unusual meteorological events on avian breeding biology. Moreover, I also studied whether various characteristics of local weather influence the nestlings' sex ratio at fledging age or differently affect the growth of male and female offspring.

Methods

Study species

The House Sparrow belongs to the passerines (order Passeriformes), in the family of Old World Sparrows (Passeridae). They have about 25-30 grams weight, and about 15 centimeters length. Males and females are sexually dimorphic at adulthood (Figure 1.), but sexes look alike until the first molt (Figure 2, Figure 3).

As a human commensalist, House Sparrow has accompanied man for centuries and became the most successfully urbanized bird (Shaw, Chamberlain & Evans 2008). In the last decades, number of House Sparrows has decreased in several areas of the world, but most dramatically in Western-Europe. The biggest decline was recorded in some metropolitan areas (De Laet & Summers-Smith, 2007), but the reasons are still unknown. This decreasing trend is also observable in Hungary (Seress *et al.* manuscript), with a moderate decline (3 %) over the past eleven years (http://mpc.mme.hu/charts/trends).

House Sparrows breed in human settlements. It is a non-migrant social species; individuals feed in flocks even in the breeding season. Although the adults are primarily granivorous, feeding on a wide variety of seeds, nestlings are mostly provisioned with insects and caterpillars; Orthoptera, Diptera, Hymenoptera, Hemiptera, Lepidoptera, Arachnida preys are typical (Anderson 2006).

Males choose nesting sites in early spring, and try to attract a mate by singing. Clutches usually contain 3-6 eggs, which are incubated by both parents for 11-14 days. Nestlings are altricial; they are provisioned by both parents for another 11-14 days in the nest, and for one or two weeks after they fledged. Members of a pair usually stay together in the breeding season, and they can raise up to three or four clutches in one season.

Earlier studies showed that weather conditions presumably affect the House Sparrow parents' investment and the survival of the nestlings as well (Peach *et al.* 2008).Weather conditions documentedly affect the provisioning rate of House Sparrow parents (Pipoly, Bókony & Liker 2011), which can influence the development of the nestlings. The effect of climatic conditions on House Sparrow fledgling's body size have also reported (Ringsby *et al.* 2002).

The species is in the Least Concern category based on The IUCN Red List, but it is a protected species in Hungary since 9th May, 2001, as a notable species for conservation in the European Union.

Figure 1: Banded adult House Sparrow female (left) and male (right) (Kittenberger Zoological Garden, Veszprém; photos by A. Liker)

Figure 2: House Sparrow nestlings at the age of 3 days (Photographed by I. Pipoly)

Figure 3: House Sparrow nestlings at the age of fledging (Photographed by G. Seress)

Study area and the House Sparrow population

House Sparrows were studied in a nestbox-breeding population in the Kittenberger Zoological Garden of Veszprém (Veszprém, Hungary; N 47°05'32", E 17°53'44"). Nest-boxes were erected 3-6 meters above ground, mostly on tree trunks (Figure 4). The House Sparrow population in this study area has been studied since 2004. Some of the breeding birds are individually marked with one numbered aluminium band, and three coloured plastic bands (Figure 1 & 2). There are about a hundred nest-boxes at the study area, in which 50-70 breeding episodes were registered per year. Multiple reproductive attempts in the same breeding season are frequent in the population.

Figure 4: Part of the study area with some nest-boxes (Photographed by V. Bókony)

Data collection

Breeding of the House Sparrows was monitored between the middle of April and early August each year from 2005 to 2010 by the Ornithology Research Group at University of Pannonia. Each nest box was checked two or three times a week, and the number of eggs or nestlings and the age of the nestlings were registered. Date of laying was estimated from the number of eggs in the clutch found during egg laying or from the day of hatching assuming an 11-days average incubation period length. Day of hatching was known for several nests or it was estimated from the developmental state of nestlings when hatching has occured in the inter-monitoring interval. Nestlings were banded before they fledged at the age of 10.2 ± 0.1 days (mean $\pm$ SE; Figure 3 & 5), using an individual combination of rings as in adults. Upon ringing, nestlings were measured; the body weight was measured in grams (± 0.1 g) by a spring balance, and the left tarsus length was measured in millimeters (± 0.1 mm) by a vernier caliper (Figure 5). In 2005-2007, a drop of blood was taken from each ringed nestling with insuline needle, and stored in 1.5 ml Queen's lysis buffer.

Figure 5: Measuring methods; Body weight measuring (left); tarsus length measuring (right) (Measuring person: G. Seress; photos by I. Pipoly)

Meteorological data were collected by a nearby meteorological station, about 2800 meters from the study area (Lajos Takács, Vmeteo Club, Veszprém). Daily minimum temperature (°C), daily maximum temperature (°C) and daily precipitation (mm) were measured in a standardized way from 2005 to 2010. Additionally, temperature was recorded three times per day, at 6:00, 14:00 and 22:00 hours.

Offspring sexing

Information about the sex of the offspring originated from two sources. On the one hand, sex was known from House Sparrow recapture / resighting data from the study area for n=88 individuals (48 males, 40 females). On the other hand, offspring sex was diagnosed from the blood samples by molecular methods for n=236 individuals (140 males, 145 females).

Blood samples taken in 2005-2007 were stored in Queen's lysis buffer at room temperature in Veszprém until the laboratory analysis. Because this procedure is costly, we did not sex all nestlings from the population for which we had samples; instead we chose 236 birds of the total 419 randomly, with the constraint that they cover 60 clutches, 20 from each year. We always sexed whole broods, i.e. each nestling alive at the age of ringing in a given nest was sexed. Samples were analysed in 2011 in the molecular laboratory of the Department of Ecology, Institute of Biology, Faculty of Veterinary, Szent István University, Budapest.

From each sample (blood plus buffer), 400 µl was treated with 15 µl proteinase K enzyme to split open the cells and inner membranes. DNA was extracted by following a standard phenol-chloroform extraction method. Pure DNA was stored in a freezer (-20°C) with 50 µl double labeled water after an alcoholic aggregation treatment.

Sex was determined by PCR amplification of two homologous genes: *CHD1-W* and *CHD1-Z*. The *CHD1-Z* gene occurs in both sexes whereas the *CHD1-W* gene occurs on the W sex chromosome carried only by females, the heterogametic sex in birds. Two independent PCR primer pairs were applied; P2 and P8 primers (Griffiths *et al.* 1998), and the 2550F and 2718R primers (Fridolfsson & Ellegren 1999). Both primer pairs are used for passerine sex determination. In the PCR reaction, 36 cycles were made with 25 µl sample. In a cycle, denaturation was made on 94°C, hybridization was made on 48°C and DNA synthesis was made on 72°C with the enzyme Taq polimerase. The results were evaluated after agarose gel-electrophoresis with 1 % of agarose in each gel.

To verify the molecular results, we have analysed the blood samples of N=39 individuals whose sex was known from resighting / recapture data. Molecular results showed conformity with recapture / resighting results in all but one case. The single mismatch was most likely due to an erroneous record (i.e. there was only 1 resighting of that individual).

Data analysis

Analysis of meteorological data

Daily minimum temperature, daily maximum temperature and daily precipitation data were used to create meteorological variables that caharcterize the weather conditions for the following two periods separately:

- The incubation period of clutches (from the day of laying the penultimate egg to the day of hatching).
- The development period of nestlings (from the day of hatching to the day preceding the day of banding and measuring).

The following meteorological variables were calculated:

Mean of the daily average temperatures: mean of the daily average temperature (that is the mean of the daily minimum and maximum temperatures)

Absolute minimum temperature: the lowest minimum temperature value of the period

Absolute maximum temperature: the highest maximum temperature value of the period

Number of rainy days: number of rainy days during the period

Proportion of rainy days: number of rainy days during the period divided by the length of the period

Total precipitation: sum of the precipitation in millimeters during the period

Mean daily precipitation: the sum of the precipitation in millimeters during the period divided by the length of the period

Furthermore, the following meteorological variables were calculated using either the daily maximum temperature (T_{max}), or the daily minimum temperature (T_{min}), or daily average temperature ($T_{average}$):

Variance of T: variance of the daily temperature values over the period

Trend of T: difference in the mean of daily temperature values between the first and the second half of the period (this value is positive if the first half of the period was warmer and, negative if the second half of the period was cooler)

Cumulative rise of T: sum of the temperature increases from one day to the next during the period (i.e. it only includes the positive changes during the period)

Cumulative drop of T: sum of the temperature drops from one day to the next during the period (i.e. it only includes the negative changes during the period)

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Mean rise of T: the mean of temperature rises from one day to the next during the period (including only positive changes)

Mean drop of T: the mean of temperature drops from one day to the next during the period (including only negative changes)

Maximum rise of T: the highest temperature increase from one day to the next during the period

Maximum drop of T: the biggest temperature drop from one day to the next during the period

Number of rises in T: number of the temperature increases from one day to the next during the period

Proportion of rises in T: number of days when the temperature increased from one day to the next during the period, divided by the length of the period

Number of drops in T: number of the temperature drops from one day to the next during the period

Proportion of drops in T: number of the temperature drops from one day to the next during the period divided by the length of the period

Extremely cold days: number of unusually cold days, i.e. data points under the 90 % confidence limits of the quadratic regression curve of temperature in relation to date, using our 6-years database of daily temperature data between 1st April and 31st August each year

Extremely warm days: number of unusually warm days, i.e. data points above the 90 % confidence limits of the quadratic regression curve of temperature in relation to date, using our 6-years database of daily temperature data between 1st April and 31st August each year

Proportion of extremely cold days: number of unusually cold days divided by the length of the period

Proportion of extremely warm days: number of unusually warm days divided by the length of the period

Because many of these variables are inter-correlated, to avoid multicolinearity we used principal component analysis (PCA) to reduce the number of dimensions and obtain uncorrelated variables that express the main axes of meteorological variability. This method uses the standardized covariance matrix of the data to calculate linear combinations of the original variables – these new variables are the principal components (PCs). This analysis resulted in 12 principal components, from which the first four explained 59.58 % of total variance. The rest of the PCs had low explanatory power and weak correlations with

meteorological variables and were hard to interpret. Henceforth, the first four PCs were used in all the further analyses as proxies for main aspects of weather conditions (Table 1). The interpretation of PCs was based on the loadings, i.e. the correlation between the PC and the original weather variables, focusing on "large" effects. In ecological and evolutionary studies a "large" effect has a Pearson product's correlation coefficient (r) of at least 0.50, whereas effects with $0.1 < r < 0.3$ and $r < 0.1$ are considered as "medium" and "small", respectively (Møller & Jennions 2002). The interpretations of the four principal components are as follows:

PC1 – "variability": correlates positively with high variance in temperatures, high cumulative, maximum and mean changes in temperature in both directions (i.e. cooling and warming), high number of unexpectedly cool days, and high number of temperature rises from one day to the next. Thus this PC may reflect the amount of variability in temperature during spring and summer when most variation results from gradually rising temperatures and occasionally occurring large temperature drops (Table 1).

PC2 – "cooling": correlates positively with high number of temperature drops, and decreasing temperature trends (i.e. the first half of the period being warmer than the second), leading to lower average temperature. Thus this PC may express the direction of variability, i.e. how much the period can be characterized by temperature dropping from day to day (Table 1).

PC3 – "aridity": correlates positively with low number of rainy days and less total precipitation, and large changes in the daily minimum temperature. Thus this PC may describe the aridity of the period (Table 1). The relationship between daily minimum temperatures and precipitation is probably due to the buffer effects of clouds on nighttime cooling (Vera Gácser, personal communication).

PC4 – "warmth": correlates positively with high temperatures and high number of extremely warm days. Thus this PC may express the warmth of the period (Table 1).

Table 1: Loadings of the principal components; strong correlations (r>0.5) are marked with yellow

Variables	PC1	PC2	PC3	PC4
Mean of the daily average temperatures	-0.21	-0.52	0.01	0.57
Absolute minimum temperature	-0.36	-0.39	-0.21	0.55
Absolute maximum temperature	0.10	-0.48	0.03	0.66
Variance of T_{max}	0.69	0.09	-0.19	0.40
Variance of T_{min}	0.60	0.02	0.30	-0.04
Variance of $T_{average}$	0.71	0.02	-0.11	0.35
Trend of T_{max}	-0.26	0.60	0.12	0.42
Trend of T_{min}	-0.21	0.60	0.07	0.37
Trend of $T_{average}$	-0.25	0.64	0.10	0.43
Cumulative rise of T_{max}	0.86	-0.08	0.07	-0.06
Cumulative rise of T_{min}	0.53	0.06	0.58	-0.41
Cumulative rise of $T_{average}$	0.87	-0.19	0.12	-0.17
Cumulative drop of T_{max}	0.48	0.51	0.16	0.39
Cumulative drop of T_{min}	0.32	0.54	0.65	-0.05
Cumulative drop of $T_{average}$	0.46	0.55	0.23	0.42
Maximum rise of T_{max}	0.73	0.15	0.00	-0.06
Maximum rise of T_{min}	0.39	0.27	0.50	-0.41
Maximum rise of $T_{average}$	0.64	0.12	0.04	-0.12
Maximum drop of T_{max}	0.63	0.16	0.06	0.34
Maximum drop of T_{min}	0.37	0.17	0.55	-0.09
Maximum drop of $T_{average}$	0.64	0.16	0.05	0.32
Number of rises in T_{max}	0.62	-0.27	0.08	-0.24
Number of rises in T_{min}	0.45	-0.38	0.04	-0.21
Number of rises in $T_{average}$	0.54	-0.47	0.08	-0.35
Proportion of rises in T_{max}	0.53	-0.55	-0.12	-0.12
Proportion of rises in T_{min}	0.30	-0.65	-0.17	-0.08
Proportion of rises in $T_{average}$	0.42	-0.74	-0.10	-0.26
Number of drops in T_{max}	-0.24	0.60	0.35	-0.06
Number of drops in T_{min}	0.01	0.65	0.42	-0.12
Number of drops in $T_{average}$	-0.14	0.75	0.33	0.07
Proportion of drops in T_{max}	-0.47	0.59	0.19	0.07
Proportion of drops in T_{min}	-0.21	0.69	0.30	0.03
Proportion of drops in $T_{average}$	-0.33	0.76	0.18	0.22
Mean rise of T_{max}	0.53	0.19	0.02	0.14
Mean rise of T_{min}	0.28	0.31	0.58	-0.30
Mean rise of $T_{average}$	0.44	0.27	0.10	0.11
Mean drop of T_{max}	0.63	-0.05	-0.04	0.37
Mean drop of T_{min}	0.44	-0.03	0.35	0.11
Mean drop of $T_{average}$	0.59	-0.14	-0.03	0.32
Extremely cold days in $T_{average}$	0.48	0.48	-0.35	0.06
Extremely cold days in T_{min}	0.57	0.33	-0.23	-0.14
Extremely cold days in T_{max}	0.45	0.40	-0.50	0.17
Proportion of extremely cold days in $T_{average}$	0.45	0.49	-0.37	0.09
Proportion of extremely cold days in T_{min}	0.56	0.34	-0.26	-0.12
Proportion of extremely cold days in T_{max}	0.40	0.41	-0.51	0.21
Extremely warm days in $T_{average}$	0.05	-0.45	0.29	0.63
Extremely warm days in T_{min}	-0.08	-0.26	0.48	0.47
Extremely warm days in T_{max}	0.13	-0.43	0.28	0.60
Proportion of extremely warm days in $T_{average}$	0.02	-0.46	0.28	0.62
Proportion of extremely warm days in T_{min}	-0.11	-0.30	0.44	0.50
Proportion of extremely warm days in T_{max}	0.11	-0.44	0.26	0.58
Number of rainy days	0.17	0.49	-0.52	0.03
Proportion of rainy days	0.05	0.44	-0.63	0.10
Total precipitation	0.13	0.31	-0.66	0.18
Mean daily precipitation	0.03	0.29	-0.70	0.22
Eigenvalue	**10.98**	**10.13**	**5.95**	**5.71**
Variance % explained	**19.96**	**18.42**	**10.82**	**10.38**

Analysing the relationship between reproductive success and weather

Hatching success was estimated as the percentage of eggs hatched in those nests where at least one chick hatched. Fledging success was estimated as the percentage of hatched young that were alive at the age of ringing (i.e. few days before fledging) in those nests where at least one nestling reached that age. We could not use nests in which no chick hatched or no chick reached the age of ringing because the period for which the meteorological variables should be calculated was not comparable with (i.e. was much shorter than) the developmental periods of successful nests. Number of fledglings was approximated by the number of banded and measured nestlings at the age of ringing (see above), because disturbance closer to the time of fledging may cause premature leaving of the nest. Sex ratio was defined as the number of males divided by the total number of nestlings in a brood.

The data were analyzed by general or generalized mixed-effects modeling as follows:

Hatching success, fledging success and sex ratio at fledging age: Generalized linear mixed-effects models with binomial distribution were used. ID number of nestboxes and year were used as nested random factors in the models. Models of hatching success contained the number of eggs in the clutch and the date of hatching as covariates, while models of fledging success and sex ratio contained the date of hatching as covariate.

Number of hatclings and number of fledglings: Generalized linear mixed-effects models with Poisson distribution were used. ID number of nestboxes and year were used as nested random factors in the models. All models contain date of hatching as covariate.

Body mass and tarsus length of the nestlings: General linear mixed-effects models were used. The ID number of the brood, the ID number of nestboxes and year were used as nested random factors in the models. All models contain nestling age, brood size and date of hatching as covariates. To analyze sex-dependent weather effects, models also included nestlings' sex and its interactions with weather variables (PCs).

In all cases, the importance of weather variables (PCs) was assessed by model comparison based on Akaike's information criterion (AICc). This is an information-theoretic approach that simultaneously evaluates alternative models by balancing between model complexity and goodness of fit, and it is becoming widespread in ecology (Garamszegi 2010). It is useful if several variables are needed to describe the studied phenomenon, because it yields inference on an entire set of candidate models instead of one "final model" (Symonds & Moussalli 2011). The selection method is based on the difference between the AICc-value of the models: the model with the lowest AICc-value has the most support for the data (Garamszegi

2010). Several treshold values are used to decide which models are supported enough over the rest (Symonds & Moussalli 2011). In this study, the strictest treshold was applied; it means that a model is considered as supported model when the AICc difference between that given model and the „best model" (i.e. the model with the lowest AICc-value in the model set) is lower than 2. From these AICc differences, Akaike weights were calculated that express the probability that a given model is actually the best in the model set (Symonds & Moussalli 2011).

For each dependent variable, we constructed a model set that contained all possible combinations of the four PCs (15 models) and all two-way interactions of the PCs (6 models; excepting the two model sets for sex-dependent growth because in those models all PCs were used in interaction with sex). To keep the size of model sets reasonable, we did not explore all possible higher-level interactions of PCs. However, whenever model selection indicated that more than one interaction may be important, those model sets were expanded by models including more combinations of PCs. To assess the magnitude and direction of the found effects, we calculated the partial correlation coefficient (r) with 95% confidence interval for a model that contains all covariates that were included in at least one model in the set of supported models (i.e. AICc difference < 2). I chose this approach of presenting the results because averaging the parameter estimates over the supported models is inappropriate when there are interactions among predictors (Symonds & Moussalli 2011).

Linearity was tested by quadratic regression and general additive models (GAM) in those cases when graphs suggested that some relationships might be non-linear; however, these yielded the same conclusions as linear models so only the latter's results are shown here.

The R 2.12 sofware was used for all the analyses, with packages „lme4" (Bates, Maechler, & Bolker 2011) and „AICcmodavg" (Mazerolle 2012). Means are presented along with ± SE values throughout.

Results

The database about the reproductive biology of the House Sparrow population in Zoo Veszprém contains 317 broods and 736 nestlings from 2005 to 2010. Mean hatching success was 74.6 % that varied between 67.5 % and 84.4 % during the six study years. Mean fledging success was 69.1 % that varied between 56.3 % and 82.2 % during study years. 51.6 % of the eggs have become fledged nestlings. There were 317 clutches where at least one nestling hatched; the number of clutches varied between 25 and 69 per year (Table 2). Mean body mass of nestlings at the age of ringing was 21.1 ± 0.2 grams. Yearly mean of body mass varied between 19.3 ± 0.4 and 23.5 ± 0.3 grams. Mean tarsus length of nestlings was 17.4 ± 0.1 millimeters that varied between 16.8 ± 0.1 and 18.5 ± 0.1 mm yearly averages during study years. As it can be seen from these data, there was considerable variation in components of reproductive success.

Table 2: Explorative results about the reproductive biology of the study population

	2005	2006	2007	2008	2009	2010	Total
number of eggs	248	296	219	277	265	122	1427
nr. of hatched nestlings	202	227	157	187	189	103	1065
nr. of fledged nestlings	138	152	129	125	134	58	736
hatchlings / eggs	0.815	0.767	0.717	0.675	0.713	0.844	0.746
fledglings / hatchlings	0.683	0.670	0.822	0.668	0.709	0.563	0.691
fledglings / eggs	0.556	0.514	0.589	0.451	0.506	0.475	0.516
total nr. of clutches	62	69	46	59	56	25	317
nr. of hatched clutches	52	60	40	50	50	25	277
nr. of fledged clutches	46	50	38	40	40	17	231
hatched / total clutches	0.839	0.870	0.870	0.847	0.893	1.000	0.874
fledged / hatched clutches	0.885	0.833	0.950	0.800	0.800	0.680	0.834
fledged / total clutches	0.742	0.725	0.826	0.678	0.714	0.680	0.729
mean body mass (g)	23.53	20.84	21.92	19.26	20.76	19.56	21.14
mean tarsus length (mm)	18.48	17.53	17.51	16.83	17.04	17.01	17.4
known sexes (nr.)	89	97	99				285
nr. of males	40	48	52				140
nr. of females	49	49	47				145
sex ratio (males/total)	0.449	0.495	0.525				0.491
cluthes with known sex ratio	21	21	25				67

Sex was known for 285 nestlings: 140 males and 145 females. The mean sex ratio was 49.1 %, which did not differ significantly from unity overall (Binomial test: 140 males / 285 nestlings, p = 0.813) nor in any of the study years (Binomial tests: for the year 2005: 40 males / 89 nestlings, p = 0.397; for the year 2006: 48/97, p > 0.99; for the year 2007: 52/99, p = 0.688) and did not differ between years (Chi-squared test: Chi^2 = 1.0856, df = 2, p = 0.581) (Table 2, Figure 6). Primary sex ratio of 20 clutches (where all the laid eggs hatched), showed that the slight female bias observed among fledglings also existed among hatchlings, but it was also nonsignificant (Binomial test: 40 males / 85 nestlings, 47%; p = 0.665).
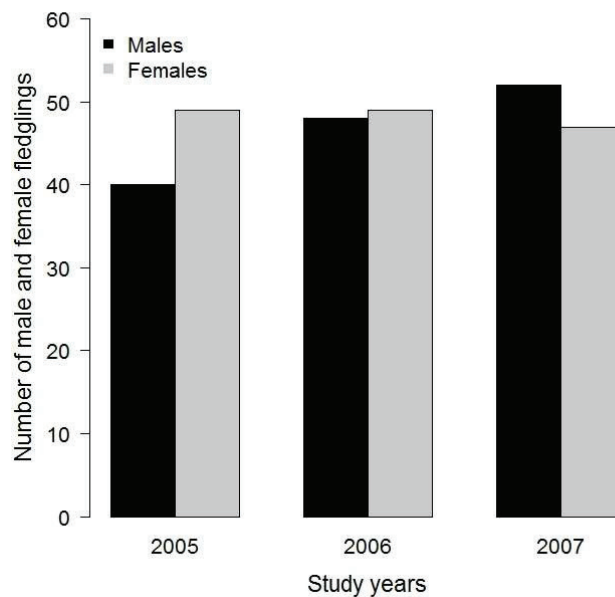
Figure 6: The number of male and female nestlings in 3 of the study years

Hatching success

Model selection supported five models (Appendix 1). The best model was the nullmodel which contains only the confounding covariates, and none of the weather variables (PCs). Hatching success was greater in smaller clutches and declined slightly over the season (Table 3). The second best model contains the interaction of PC3 – "aridity" and PC4 – "warmth". This interaction of medium effect size shows that hatching success was greatest when there were many dry and warm days during the incubation period, and it was smallest in wet and warm weather (Figure 7) The rest of the supported models each contain a PC with small effect size (Table 3).

Table 3: Effect size estimates (r= partial correlation coefficient, CI= 95% confidence interval) for hatching success; n=261 nests. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	z-value	r	CI lower	CI upper
intercept	3.599	0.22	0.10	0.33
nr. of eggs	-2.773	-0.17	-0.29	-0.05
PC3:PC4	2.212	0.14	0.02	0.26
PC3	1.031	0.06	-0.06	0.18
PC4	-0.471	-0.03	-0.15	0.09
date of hatching	-0.520	-0.03	-0.15	0.09
PC2	0.171	0.01	-0.11	0.13
PC1	0.114	0.01	-0.11	0.13
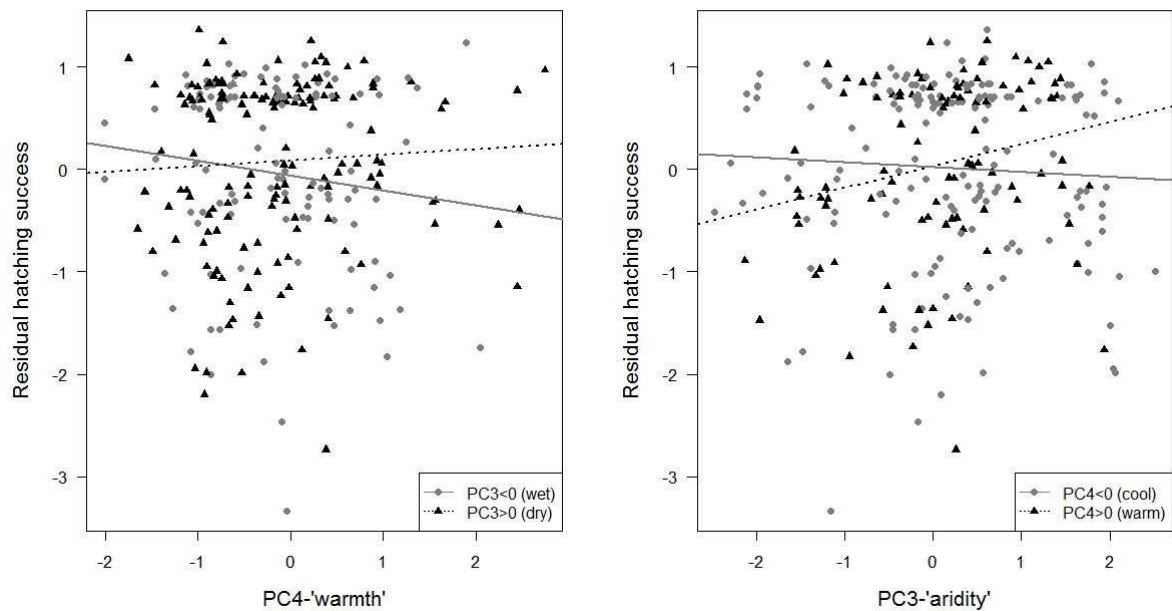
Figure 7: The relationship of hatching success with the interaction of PC3 – „aridity" and PC4 – „warmth". Hatching success was controlled for confounding variables (number of eggs and date of hatching); n=261 nests.

Number of hatchlings

Out of the five supported models (Appendix 2), the best model was the nullmodel (containing only the date of hatching) while the rest models each contained one of the four PCs. All these effects were small (Table 4).

Table 4: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for number of hatchlings; n=261 nests. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	z-value	r	CI lower	CI upper
intercept	6.77	0.39	0.28	0.49
date of hatching	-1.34	-0.08	-0.20	0.04
PC4	0.92	0.06	-0.06	0.18
PC2	-0.71	-0.04	-0.17	0.08
PC3	-0.47	-0.03	-0.15	0.09
PC1	0.48	0.03	-0.09	0.15

Fledging success

Model selection supported five models (Appendix 3). The best model contains PC2 – "cooling" and PC4 – "warmth" besides hatching date. All the other supported models also contain PC2, and all but one contain PC4; two models include their interaction. Furthermore, 3 of the supported models contain PC1 – "variability", two of them in interaction with PC2. These results suggest that fledging success decreased with the frequency of temperature drops and increased with the frequency of warm days (Figure 8), and these two effects strengthened each other i.e. fledging success was highest in periods with many warm days and little "cooling" (Figure 9). However, frequent "cooling" reduced fledging success only when it resulted in high variability, i.e. when temperature changes were large (Figure 10). Thus, "variability" can increase fledging success if this variability is represented by warming (Figure 10). Fledging success was lower at the end of the breeding season (Table 5).

Table 5: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for fledging success; n=221 nests. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	z-value	r	CI lower	CI upper
intercept	4.86	0.32	0.19	0.43
date of hatching	-2.70	-0.18	-0.31	-0.05
PC1:PC2	-1.91	-0.13	-0.26	0.00
PC2:PC4	-1.31	-0.09	-0.22	0.04
PC4	1.04	0.07	-0.06	0.20
PC2	-0.80	-0.05	-0.19	0.08
PC1	0.15	0.01	-0.12	0.14
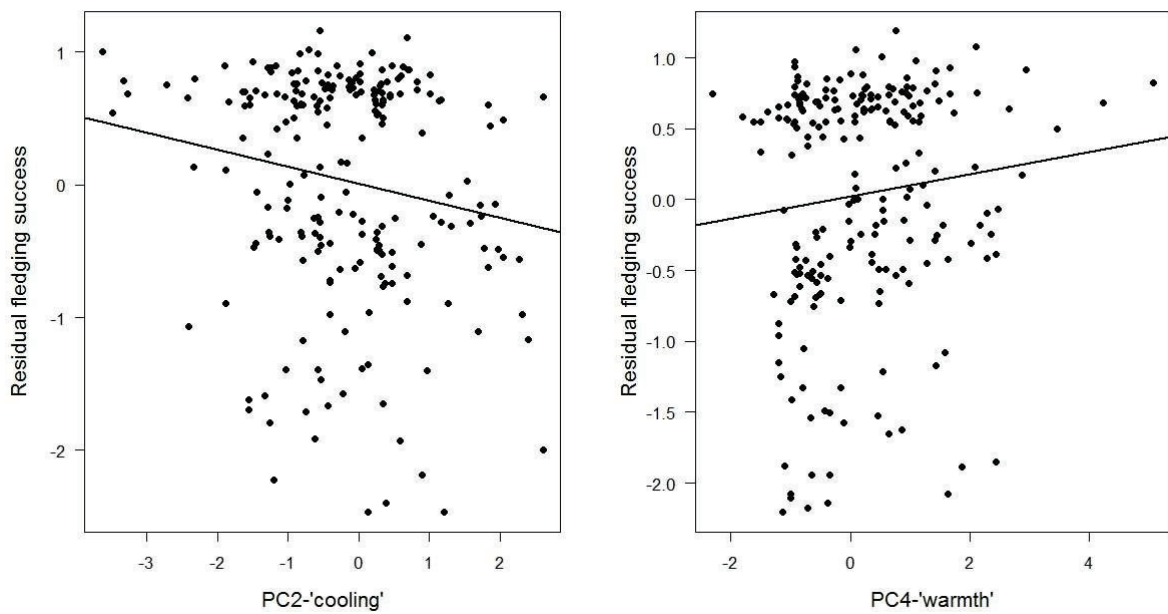
Figure 8: The relationship of fledging success with PC2 – „cooling" (left) and with PC4 – „warmth" (right); Fledging success was controlled for confounding variables (date of hatching and PC4 for the relationship with PC2; date of hatching and PC2 for the relationship with PC4); n=221 nests
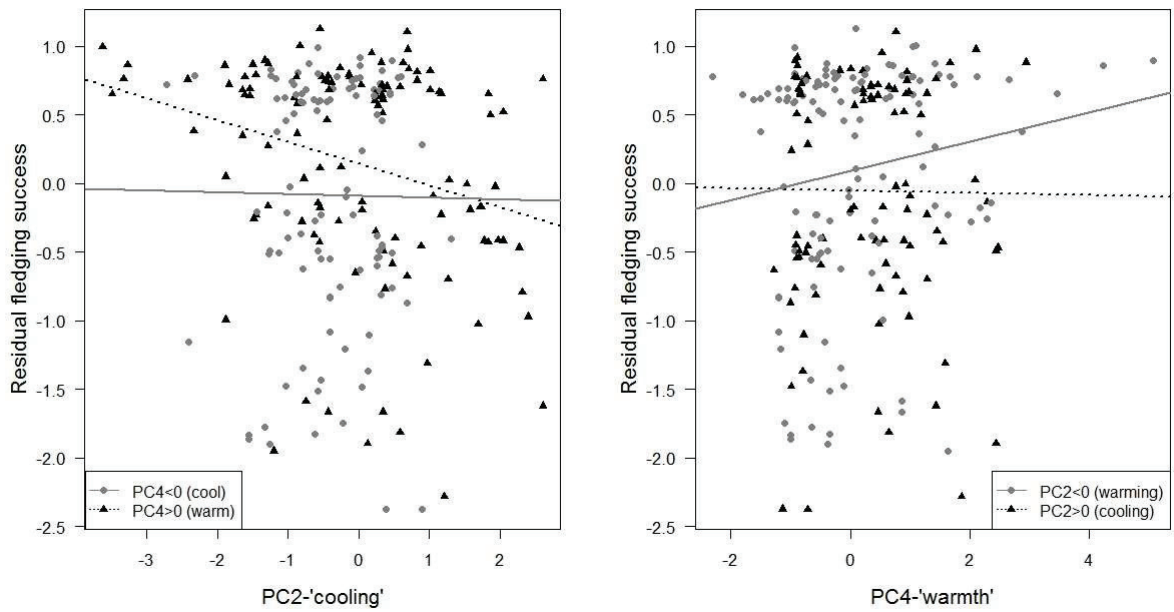
Figure 9: The relationship of fledging success with the interaction of PC2 – „cooling" and PC4 – „warmth"; Fledging success was controlled for date of hatching; n=221 nests
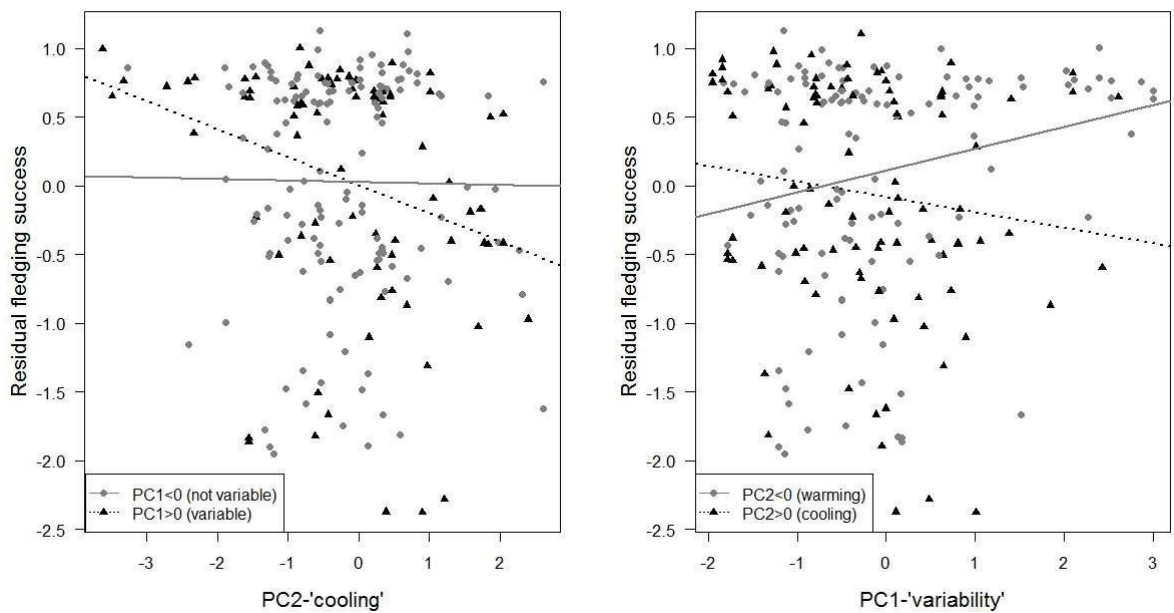
Figure 10: The relationship of fledging success with the interaction of PC1 – „variability" and PC2 – „cooling". Fledging success was controlled for date of hatching; n=221 nests

Number of fledglings

Out of four supported models (Appendix 4), three models (including the best model) contains PC4 – "warmth". This variable has a medium effect size, showing that more nestlings reached the fledging age when there were more warm days during their development (Table 6; Figure 11). The nullmodel was also included among the supported models, containing only the date of hatching. Clutches that hatched earlier in the season produced a greater number of fledglings (Table 6). The effects of PC1 and PC3 were small (Table 6).

Table 6: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for number of fledglings; n=221 nests. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	z-value	r	CI lower	CI upper
intercept	6.75	0.42	0.30	0.52
date of hatching	-2.18	-0.15	-0.27	-0.02
PC4	1.77	0.12	-0.01	0.25
PC3	-1.03	-0.07	-0.20	0.06
PC1	0.63	0.04	-0.09	0.17
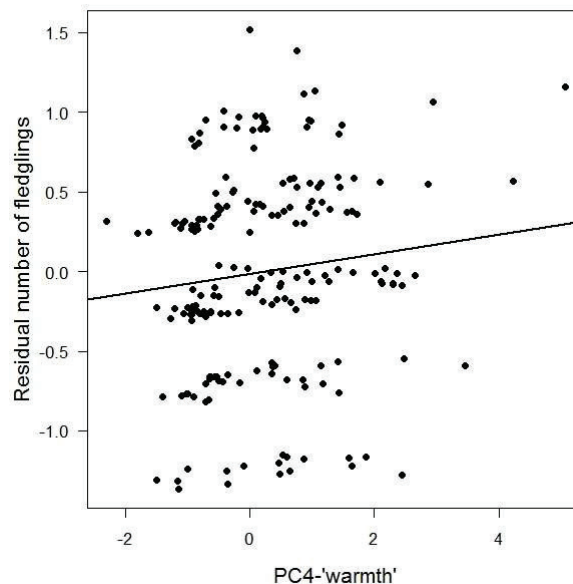
Figure 11: The relationship of number of fledglings with PC4 - „warmth". Number of fledglings was controlled for date of hatching; n=221 nests

Body mass of the nestlings

Model selection supported two models (Appendix 5), both containing PC3 – "aridity" and the interaction of PC2 – "cooling" and PC4 – "warmth". These medium-small effects show that nestlings reached lower mass in wetter weather (Table 7; Figure 12) and greater mass in warmer weather but only when there were also coolings (Figure 13). Nestlings that hatched earlier in the season and those weighed at older age had greater body mass, whereas brood size and PC1 – "variability" had little effect (Table 7).

Table 7: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for the body mass of the nestlings; n=693 nestlings. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	t-value	r	CI lower	CI upper
intercept	7.10	0.26	0.19	0.33
PC2	-3.35	-0.13	-0.20	-0.05
age of nestlings	2.74	0.10	0.03	0.18
PC2:PC4	2.66	0.10	0.03	0.17
PC4	2.63	0.10	0.03	0.17
date of hatching	-2.40	-0.09	-0.17	-0.02
PC3	2.30	0.09	0.01	0.16
PC1	-0.95	-0.04	-0.11	0.04
nr. of fledglings	0.15	0.01	-0.07	0.08
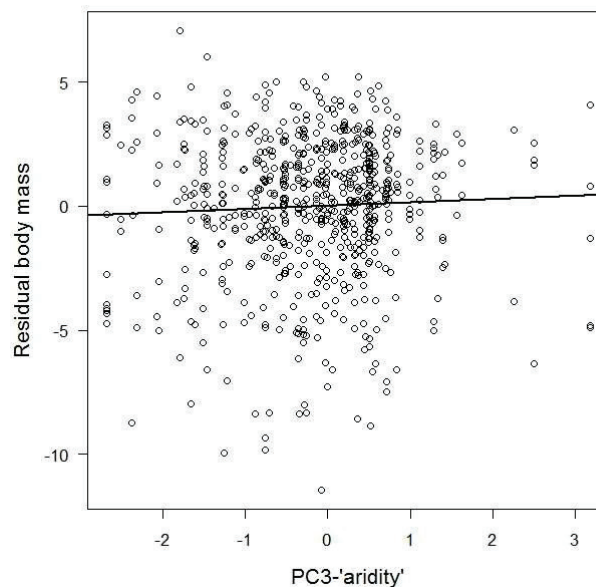
Figure 12: The relationship of body mass with PC3 – „aridity". Body mass of the nestlings was controlled for confounding variables (interaction of PC2 and PC4, date of hatching, age and number of fledglings); n=693 nestlings
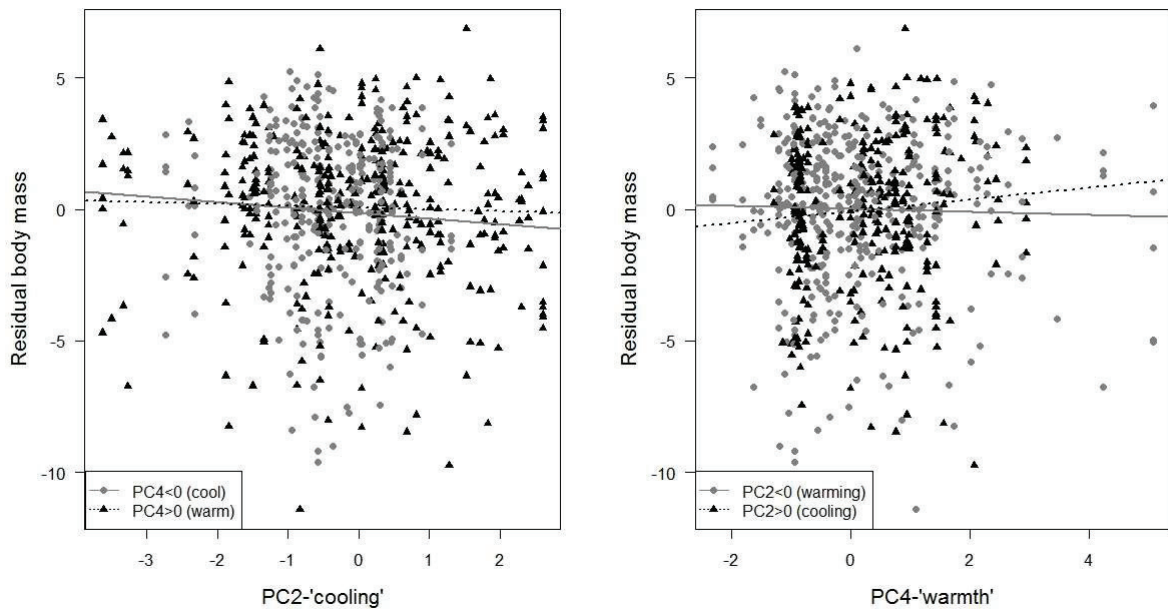
Figure 13: The relationship of body mass of the nestlings with the interaction of PC2 – „cooling" and PC4 – „warmth". Body mass of the nestlings was controlled for confounding variables (PC3 and date of hatching, age and number of fledglings); n=693 nestlings

Tarsus length of the nestlings

Model selection supported four models (Appendix 6), each of which contained PC3 – "aridity". This medium-small effect indicates that nestlings grew to smaller size in wetter weather (Table 8; Figure 14), similarly to the results on body mass above. Later hatched, older nestlings in larger broods had greater tarsus length (Table 8). The effects of PC1 – "variability" and PC2 – "cooling" were small (Table 8).

Table 8: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for the tarsus length of the nestlings; n=683 nestlings. Predictor variables are listed in decreasing order of the magnitude of their effect.

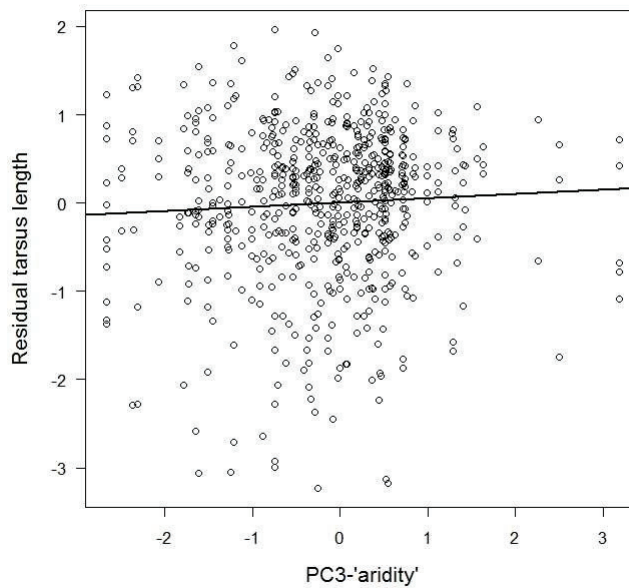| predictor	t-value	r	CI lower	CI upper
intercept	15.59	0.52	0.46	0.57
age of nestlings	5.59	0.21	0.14	0.28
date of hatching	4.73	0.18	0.11	0.25
nr. of fledglings	3.33	0.13	0.05	0.20
PC3	2.42	0.09	0.02	0.17
PC2:PC3	1.38	0.05	-0.02	0.13
PC1	0.81	0.03	-0.04	0.11
PC2	-0.23	-0.01	-0.08	0.07

Figure 14: The relationship of tarsus length with PC3 - „aridity". Tarsus length was controlled for confounding variables (date of hatching, age and number of fledglings); n=683 nestlings

Sex ratio at fledging age

Examining what factors may affect the sex ratio of the nestlings at fledging age, uncertainty about the best model was relatively high: 9 supported models were found (Appendix 7), one of which was the nullmodel. The best model contains PC1 – "variability" and PC3 – "aridity"; both of these predictors occur in 7 of the supported models (also their interaction in two cases). Further, 3 models contain PC – "cooling" and 2 models contain PC4 – "warmth". All these effects are medium-sized (Table 9). The proportion of males decreased when the weather was more variable and more dry (Figure 15), and these two effects seemed to strengthen each other (Figure 16). Frequent "cooling" also decreased the proportion of males, but greater "warmth" increased the proportion of males (Figure 15). Fewer males fledged at the end of the reproductive season than at earlier dates (Table 9).

Table 9: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for the sex ratio at fledging age; n=63 nests. Predictor variables are listed in decreasing order of the magnitude of their effect.

predictor	z-value	r	CI lower	CI upper
intercept	2.25	0.29	0.05	0.50
PC3	-2.59	-0.33	-0.54	-0.09
PC1	-2.52	-0.32	-0.53	-0.08
date of hatching	-2.35	-0.30	-0.51	-0.06
PC2	-2.02	-0.26	-0.48	-0.02
PC1:PC3	-1.41	-0.19	-0.42	0.06
PC4	0.99	0.13	-0.12	0.37
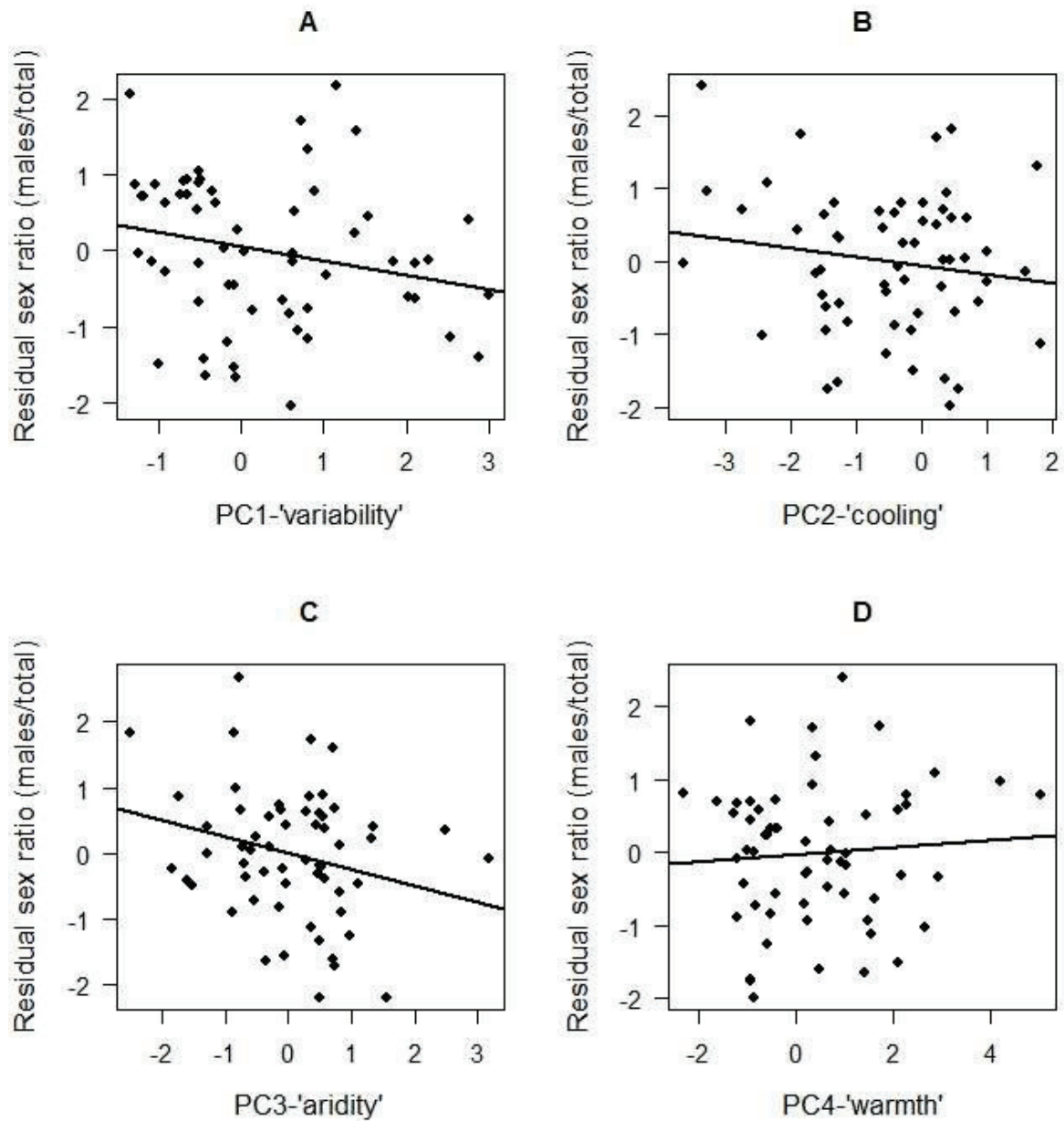
Figure 15: The relationship of sex ratio with the four main aspects of weather. Sex ratio was controlled for confounding variables (date of hatching and the 3 other PCs for each PC); n=63 nests

25
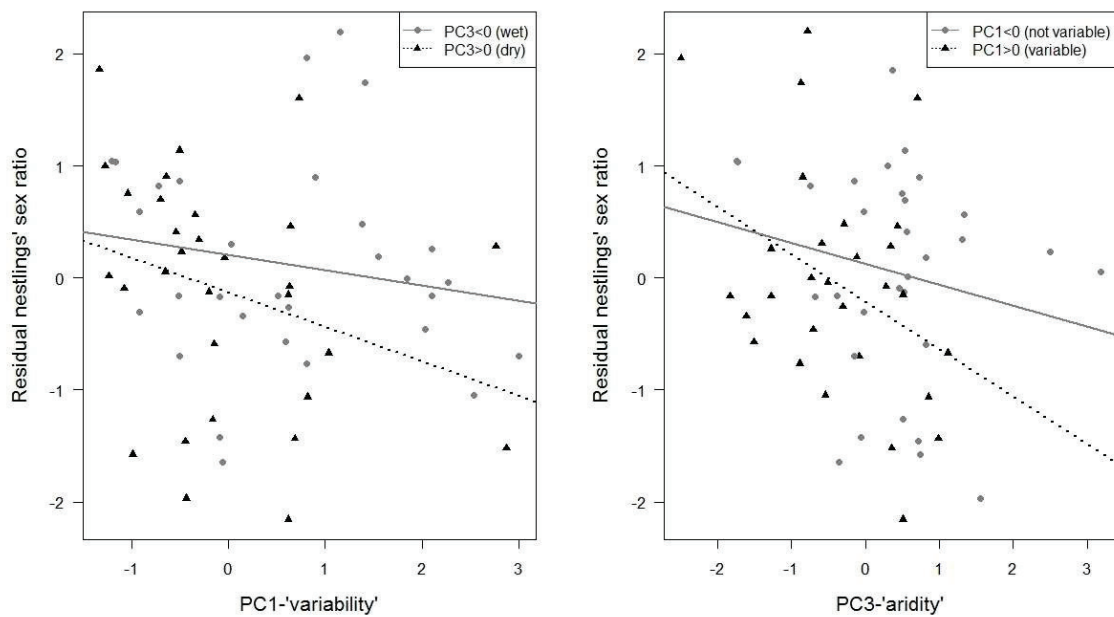
Figure 16: The relationship of sex ratio of nestlings at fledging age with the interaction of PC1 – „variability" and PC3 – „aridity". Sex ratio was controlled for confounding variables (PC2 and date of hatching); n=63 nests

Body mass in male and female nestlings

Model selection supported three models, two of which include no weather variables, whereas one model contains the interaction of PC1 – "variability" and the sex of the nestlings (Appendix 8). This medium-small effect suggests that body mass increased with temperature variability in males but not in females (Table 10, Figure 17).

Table 10: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) of for the body mass in connection with nestlings' sex; n=268 nestlings. Predictor variables are listed in decreasing order of the magnitude of their effect

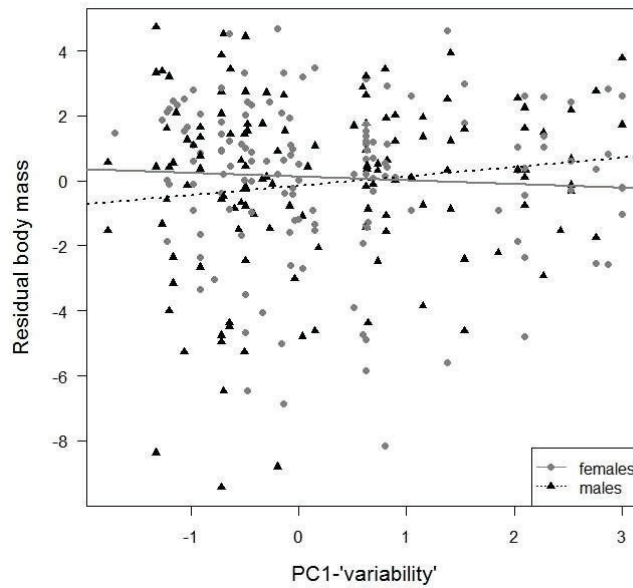| predictor	t-value	r	CI lower	CI upper
intercept	4.81	0.29	0.17	0.39
PC1	2.65	0.16	0.04	0.28
PC1:sex	-1.69	-0.10	-0.22	0.02
sex	1.04	0.06	-0.06	0.18
nr. of fledglings	-0.90	-0.06	-0.17	0.06
age of nestlings	-0.20	-0.01	-0.13	0.11
date of hatching	0.06	0.00	-0.12	0.12

Figure 17: The relationship of body mass with PC1 – „variability" for male and female nestlings. Body mass was controlled for confounding variables (date of hatching, age and number of fledglings); n=268 nestlings

Tarsus length in male and female nestlings

These results were qualitatively similar to those on body mass above: out of the 3 supported models, two included no weather variables, whereas one model showed that tarsus length increased with temperature variability in males but not in females (Appendix 9; Table 11, Figure 18).

Table 11: Effect size estimates (r= partial correlation coefficient, CI= 95 % confidence interval) for the tarsus length in connection with nestlings' sex; n=264 nestlings. Predictor variables are listed in decreasing order of the magnitude of their effect

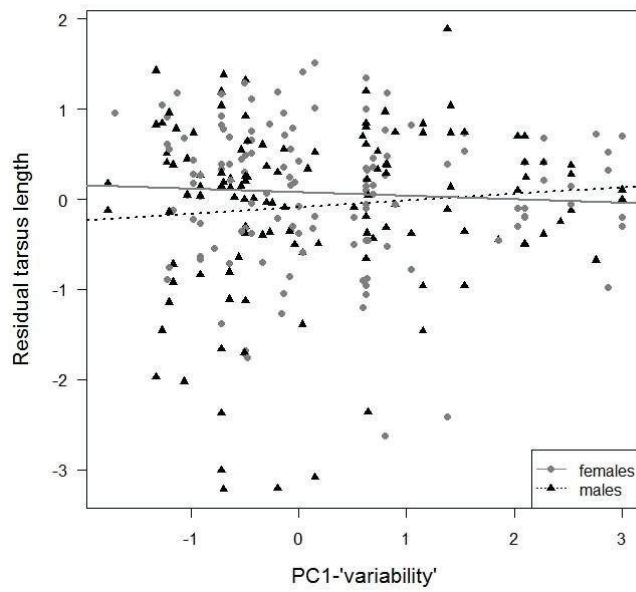| predictor	t-value	r	CI lower	CI upper
intercept	9.53	0.51	0.42	0.60
date of hatching	3.19	0.20	0.08	0.31
age of nestlings	2.82	0.17	0.06	0.29
sex	1.71	0.11	-0.01	0.22
PC1	1.63	0.10	-0.02	0.22
PC1:sex	-1.39	-0.09	-0.21	0.03
nr. of fledglings	1.04	0.07	-0.06	0.18

Figure 18: The relationship of tarsus length with PC1 – „variability" for male and female nestlings. Tarsus length was controlled for confounding variables (date of hatching, age and number of fledglings); n=264 nestlings

Discussion

My results suggest that weather conditions affect the reproductive success of House Sparrows at various levels. Dry and warm weather is favourable during the incubation period, and promote nestling development, too. Sex ratio at the pre-fledging age was also influenced by weather conditions. Overall, the effects of meteorological variables were small and they often interacted in a complex way. Note that small effects are common in ecological studies: in a sample studied by Møller & Jennions (2002) average effect size was between r=0.180 and 0.193.

Hatching success decreased in rainy weather with more warm days, while it increased with dry, warm weather. Damp warm conditions often increase microbial loads on eggshells (Beissinger, Cook & Arendt 2005). Bacteria and fungi abundance can increase the probability of trans-shell infection, thereby decreasing egg viability and hatching success (Cook *et al.* 2004; Beissinger *et al.* 2005). Cook et al. (2004) examined the effect of microbial infection and exposure of eggs to ambient temperature using cleaned and uncleaned eggs in different study sites with different temperature features. They state water presence is important for growth and transport of microbes. They have found that microbial abundance on eggshells was greater at the humid, cool study sites, and the hatching success was the greatest by cleaned eggs held on the cool site, while the second greatest hatching success was measured on the cool site with uncleaned eggs. This result suggest that infection and ambient temperature both affect the hatching success, but these factors can affect independently (Cook *et al.* 2004). This study was done under tropical climate conditions where mean temperature is higher than in temperate areas, hence cool sites may be more advantageous for egg viability there, compared to the results of our study population in the temperate zone, where warm days were more advantageous for hatching success.

Fledging success was also influenced by weather conditions. Greatest fledging success was recordable when there were a lot of warm days and few temperature drops during the nestling development period. „Cooling" was the most disadvantageous when „variability" was great (i.e. when the changes in temperature were large). These results suggest that „warmth" is beneficial for nestlings in our study area, at least within the range of temperatures spanned by our data. Note that „warmth" includes unusually high temperature for that time of season in this study and not heat on an absolute scale (e.g. days with >30 °C); further studies are needed to explore whether extreme heat is harmful for sparrows. Warm temperature may allow both nestlings and parents to invest less energy into thermoregulation, thus probability of

successful fledging may increase. The inner core temperature of several passerine species is about 40,5 °C (Kendeigh 1969). Studies suggest that house sparrow nestlings may be able to maintain relatively high body temperature only from the age of 10 days; isolated nestlings at 6 days old age lost temperature rapidly during a 15 min period (Anderson 2006). Metabolic rate of nestlings increases with temperature, but it is also increasing strongly when body temperature becomes suboptimal, i.e. when nestlings are chilling (Webb & King 1983; Anderson 2006), so colder weather may require more energy input for the same development and/or survival compared to warmer weather. This might explain why more nestlings could be raised until fledging when weather was warm on the average.

Relatively cool weather and „variability" (i.e. the magnitude of temperature drops) did not affect hatching succes, while fledging success was affected by these weather factors. Furthermore, the number of hatchlings was not influenced by weather variables at all in our study. These results suggest that incubation may act as a strong buffer against ambient weather conditions, whereas nestlings may experience more exposure to ambient weather conditions than eggs. Parents could make presumably less brooding during nestling development period (compared with egg incubation period), maybe because they must collect food for the nestlings and for themselves as well. This may manifest in lower fledging success (e. g. increased mortality) when weather is unfavourable. Another possible explanation is that nestlings might be more sensitive to weather variability than eggs, e.g. because of stricter temperature range tolerance or faster metabolism. The lower critical temperature of standard metabolism is about 21 °C while the upper range of thermal tolerance is about 47 °C by adult House Sparrows (Kendeigh 1969).

Nestlings grew smaller in wetter weather by both measures (body mass and tarsus length). The development of the nestlings probably was influenced by indirect effects of wet weather. Parents might not be able to collect enough food under unfavourable weather conditions, e. g. flight is impossible in heavy rain, or insects may be not discoverable in cloudy and/or rainy weather because they are hidden and immobile. In altricial birds, nestling growth (mass and tarsus as well) is dependent on the provisioning by the parents. In House Sparrows, investment by both parents is required to maximize their reproductive success (Hoi, Vaclav & Slobodova 2003). Unfavourable weather conditions documentedly affect the provisioning rate of male parents (Pipoly *et al.* 2011) which may cause lower body mass or greater mortality of nestlings. Food restriction can be detrimental to chick development and survival, especially if it occurs at young age (Lepczyk & Karasov 2000). Nestlings' diet contains animal material

mostly over 80 %, while the rest is mostly seeds. The proportion of animal material tends to decrease with nestling age (Anderson 2006; Brzek *et al.* 2009). Arthropod food seems to be important to younger nestlings. Weather can affect the activity and abundance of many arthropod taxa. There is a critically low temperature for most insects, under which they are not able to fly (this threshold temperature can alter with taxon). Over the threshold temperature flight is less affected by temperature (Taylor 1963). Rain might also inhibits insects' flight, because temperature usually declines when rain falls, and crashing with raindrops might be a serious challenge to an insect.

Besides the negative effect of rainy weather, the body mass of the nestlings also increased with warmer temperatures, but interestingly, this effect was more pronounced when temperature drops were also frequent during chick development. When temperature is in the suboptimal range for the nestlings they may not develop at the maximal rate as they probably must invest much energy into thermoregulation (see above) which might hinder the accumulation of body mass. Therefore frequent drops in temperature may be beneficial in warmer periods, and/or vica versa, frequent warm days may be beneficial when there the weather is otherwise cooling.

Thus, both the direct effects of weather on nestlings (i.e. metabolic costs due to suboptimal temperatures) and the indirect effects due to food availability and parental provisioning can play important role in nestlings' growth and fledging success. It is possible that hypotherm state of nestlings and decreased provisioning rate of parents act together in cool and rainy weather, resulting in fewer and smaller nestlings.

Among the weather effects I found, the strongest ones appeared in the case of fledglings' sex ratio. Processes causing bias in sex ratio can act via direct ways (e.g. nestling survival) and/or indirect ways (e. g. differential parental effort). One sex can be more sensitive to the environmental conditions than the other sex, but there is no general rule for which sex should be more sensitive, and which factors play a role in this process. Whether male or female offspring are more sensitive to unfavorable conditions varies among species (e.g. Kilner 1998, Rosivall *et al.* 2010). Furthermore, offspring sex ratio can be altered also by differential parental investment. For example, parents in species with higher male reproductive variance benefit by producing sons under favourable conditions (e.g. Ligon & Hill 2010, Dijkstra *et al.* 2010). According to the results of my study, proportion of male nestlings decreased with increasing frequency of "cooling" and with relatively high temperature variability and "aridity". Especially low proportion of males fledged when high "variability" and "aridity"

co-occurred. One possible explanation is that the sexes may differ in sensitivity to weather conditions, although it is not clear in this case why males should be more sensitive to cooling, dry weather (or females to warming, rainy weather). For example, females might react more sensitively to microbial infections in damp warm weather (see above). Similarly, it is difficult to speculate about differential parental preference for offspring sex in different weather conditions. For example, does greater variability mean a favourable condition for producing more females or are males more worth to produce in rainy periods? The overall results of this study suggest that rainy weather is not favourable for the nestlings, although some insect species (e.g. ants) swarm before rainfalls (Dr. János Kis & Dávid Fülöp, personal communication). My analyses of both body mass and tarsus length showed that greater temperature variability increased the body size of male nestlings but slightly decreased the growth of female nestlings. This finding, coupled with the results on sex ratio detailed above, suggests that the differences between the two sexes' reactions to meteorological conditions might be complex and differ among various components of weather.

Taken together, I found that weather has complex effects on the reproductive success of House Sparrows. Its components affect the rate of hatching and fledging success as well as the development of nestlings in our study population. Similar studies would promote our understanding of the effects of weather and climate on animals. Such studies are important because weather cannot be omitted from ecosystems and it can affect the population dynamics of species at multiple levels.

Summary

The effects of climatic changes on various behaviors of animals have been documented, but there is still little information about how the weather variability and extreme meteorological events influence reproductive success in birds.

In this study I have investigated the relationship between the ambient weather variability and the reproductive success of House Sparrows. The studied population breeds in a nest-box colony in the Zoo Veszprém. We monitored the breeding attempts from 2005 to 2010. Nestlings' sex was identified by molecular sexing methods in a subset of broods.

My results show that dry, warm weather is favourable during the incubation period, and promote fledging and nestling development after hatching, too. Fledging success increased with the frequency of warm days and decreased when temperature drops were frequent. Nestlings' body size was smaller in wetter weather. There were more male nestlings under less variable, warmer and less dry weather conditions. Nestlings' sex ratio did not differ from 1:1 in the study population.

Damp warm weather may be disadvantageous for hatching success as it can favour microbial infections through the eggshell. Cold and wet weather may negatively affect nestling development and survival directly through the thermoregulation of nestlings and/or indirectly by decreasing food availability or parental provisioning rate. Male and female nestlings might be differentially sensitive to weather conditions.

Weather probably has complex effects on the reproductive success of House Sparrows. It is worth to examine the deeper mechanisms of the effects of weather on different levels of avian reproductive biology.

Összefoglaló

A napjainkban zajló klímaváltozás igazoltan hatással van az állatok viselkedésére, azonban egyelőre keveset tudunk arról, hogy az időjárás változatossága és az időjárási szélsőségek hogyan befolyásolják a madarak szaporodási sikerét, és az egyes fajok hogyan képesek alkalmazkodni a szélsőséges időjárási eseményekhez.

Jelen vizsgálat a lokális időjárási változatosság és a szaporodási siker közötti kapcsolatot keresi házi verebeknél. A Veszprémi Állatkertben mesterséges odútelepen fészkelő madarak szaporodási sikeréről és a fiókák méretéről 2005 és 2010 között gyűjtöttük az adatokat. A fiókák ivararányát DNS-alapú molekuláris módszerrel határoztuk meg.

A vizsgálat eredménye szerint a száraz, meleg napok kedvezőek a kotlás és a fiókanevelés ideje alatt is.. A kirepülési siker nőtt a meleg napok számával, és csökkent ha a lehűlések gyakoribbak voltak. A fiókák testmérete (tömeg és csüdhossz) kisebb volt esős időjárás esetén. Kevésbé változatos, nedves és melegebb időjárás esetén nagyobb a hímek aránya. A fiókák ivararánya nem tér el az 1:1 aránytól a vizsgált populációban.

A nedves meleg környezet kedvezhet a mikrobiális fertőzéseknek, ami okozhatja a kelési siker csökkenését. A hideg és esős időjárás negatívan hathat a fiókák fejlődésére és túlélésére közvetlenül a fiókák hőháztartására gyakorolt hatással, illetve közvetetten a csökkenő táplálék-elérhetőséget (rovarok) vagy a szülők csökkent etetési aktivitását okozva. Úgy tűnik, az ivarok eltérően reagálhatnak az időjárás variabilitására.

Az időjárási tényezők összetett módon hathatnak a házi verebek szaporodási sikerére. Az időjárási változatosság hatásának mechanizmusait fontos lenne részletesebben megérteni a madarak szaporodásbiológiájának több szintjén, így jobban prediktálhatnánk a fajok populáció dinamikájának esetleges változásait.

Acknowledgements

University of Pannonia
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Appendices

Appendix 1: Model set for hatching success; supported models are written in bold

variables included in the models	AICc value	AICc difference	Akaike weights
nr. of eggs+hatching date	**367.54**	**0.00**	**0.19**
PC3*PC4+nr. of eggs+hatching date	**368.22**	**0.68**	**0.13**
PC1+nr. of eggs+hatching date	**369.23**	**1.69**	**0.08**
PC2+nr. of eggs+hatching date	**369.48**	**1.94**	**0.07**
PC3+nr. of eggs+hatching date	**369.49**	**1.95**	**0.07**
PC4+nr. of eggs+hatching date	369.63	2.09	0.07
PC3*PC4+PC2+nr. of eggs+hatching date	370.33	2.79	0.05
PC3*PC4+PC1+nr. of eggs+hatching date	370.35	2.81	0.05
PC1+PC2+nr. of eggs+hatching date	371.18	3.64	0.03
PC1+PC3+nr. of eggs+hatching date	371.19	3.65	0.03
PC1+PC4+hatching date	371.33	3.79	0.03
PC2+PC3+nr. of eggs+hatching date	371.42	3.88	0.03
PC2+PC4+nr. of eggs+hatching date	371.55	4.01	0.03
PC3+PC4+nr. of eggs+hatching date	371.60	4.06	0.02
PC3*PC4+PC1+PC2+nr. of eggs+hatching date	372.48	4.94	0.02
PC2*PC3+nr. of eggs+hatching date	372.54	5.00	0.02
PC1*PC3+nr. of eggs+hatching date	372.82	5.28	0.01
PC2*PC4+nr. of eggs+hatching date	372.88	5.34	0.01
PC1+PC2+PC3+nr. of eggs+hatching date	373.13	5.59	0.01
PC1*PC4+nr. of eggs+hatching date	373.13	5.59	0.01
PC1+PC2+PC4+nr. of eggs+hatching date	373.26	5.72	0.01
PC1*PC2+nr. of eggs+hatching date	373.29	5.75	0.01
PC1+PC3+PC4+nr. of eggs+hatching date	373.32	5.78	0.01
PC2+PC3+PC4+nr. of eggs+hatching date	373.52	5.98	0.01
PC1+PC2+PC3+PC4+nr. of eggs+hatching date	375.25	7.71	0.00

Appendix 2: Model set for number of hatchlings; supported models are written in bold

variables involved in the models	AICc value	AICc difference	Akaike weights
hatching date	**94.96**	**0.00**	**0.23**
PC4+hatching date	**96.57**	**1.61**	**0.10**
PC2+hatching date	**96.79**	**1.83**	**0.09**
PC1+hatching date	**96.81**	**1.85**	**0.09**
PC3+hatching date	**96.89**	**1.93**	**0.09**
PC2+PC4+hatching date	98.14	3.18	0.05
PC3+PC4+hatching date	98.41	3.45	0.04
PC1+PC4+hatching date	98.43	3.47	0.04
PC1+PC2+hatching date	98.64	3.68	0.04
PC1+PC3+hatching date	98.76	3.80	0.03
PC1+PC4+hatching date	98.76	3.80	0.03
PC3*PC4+hatching date	99.03	4.07	0.03
PC1+PC2+PC4+hatching date	100.02	5.06	0.02
PC2+PC3+PC4+hatching date	100.03	5.07	0.02
PC2*PC3+hatching date	100.21	5.25	0.02
PC2*PC4+hatching date	100.21	5.25	0.02
PC1+PC3+PC4+hatching date	100.30	5.34	0.02
PC1*PC4+hatching date	100.54	5.58	0.01
PC1*PC2+hatching date	100.61	5.65	0.01
PC1+PC2+PC3+hatching date	100.64	5.68	0.01
PC1*PC3+hatching date	100.83	5.87	0.01
PC1+PC2+PC3+PC4+hatching date	101.93	6.97	0.01

Appendix 3: Model set for fledging success; supported models are written in bold

variables involved in the models	AICc value	AICc difference	Akaike weights
PC2+PC4+hatching date	**290.04**	**0.00**	**0.16**
PC1+PC2+PC4+PC1:PC2+PC2:PC4+hatching date	**290.07**	**0.03**	**0.16**
PC2*PC4+hatching date	**290.31**	**0.27**	**0.14**
PC1*PC2+hatching date	**290.42**	**0.38**	**0.14**
PC1+PC2+PC4+hatching date	**291.33**	**1.29**	**0.09**
PC2+PC3+PC4+hatching date	292.15	2.11	0.06
PC2+hatching date	292.65	2.61	0.04
PC1+PC2+PC3+PC4+hatching date	293.46	3.42	0.03
PC1*PC2*PC4+hatching date	293.61	3.57	0.03
PC1+PC2+hatching date	293.87	3.83	0.02
PC1+PC4+hatching date	294.25	4.21	0.02
hatching date	294.90	4.86	0.01
PC2*PC3+hatching date	295.14	5.10	0.01
PC1+PC4+hatching date	295.42	5.38	0.01
PC2+PC3+hatching date	295.55	5.51	0.01
PC3+PC4+hatching date	295.62	5.58	0.01
PC1+PC2+PC3+hatching date	295.78	5.74	0.01
PC3+hatching date	295.94	5.90	0.01
PC1+hatching date	295.97	5.93	0.01
PC3*PC4+hatching date	296.45	6.41	0.01
PC1+PC3+PC4+hatching date	296.82	6.78	0.01
PC1+PC3+hatching date	297.03	6.99	0.00
PC1*PC3+hatching date	297.15	7.11	0.00
PC1*PC4+hatching date	297.44	7.40	0.00

Appendix 4: Model set for number of fledglings; supported models are written in bold

variables involved in the models	AICc value	AICc difference	Akaike weights
PC4+hatching date	**104.43**	**0.00**	**0.17**
hatching date	**105.21**	**0.78**	**0.11**
PC3+PC4+hatching date	**105.44**	**1.01**	**0.10**
PC1+PC4+hatching date	**106.09**	**1.66**	**0.07**
PC2+PC4+hatching date	106.54	2.11	0.06
PC3+hatching date	106.55	2.12	0.06
PC1+hatching date	106.73	2.30	0.05
PC3*PC4+hatching date	107.11	2.68	0.04
PC1+PC3+PC4+hatching date	107.18	2.75	0.04
PC2+hatching date	107.24	2.81	0.04
PC1+PC4+hatching date	107.35	2.92	0.04
PC1*PC4+hatching date	107.93	3.50	0.03
PC1+PC3+hatching date	108.13	3.70	0.03
PC1+PC2+PC4+hatching date	108.22	3.79	0.03
PC2*PC4+hatching date	108.54	4.11	0.02
PC2+PC3+hatching date	108.67	4.24	0.02
PC1+PC2+hatching date	108.75	4.32	0.02
PC1+PC2+PC3+PC4+hatching date	109.16	4.73	0.02
PC1*PC2+hatching date	109.59	5.16	0.01
PC1*PC3+hatching date	109.85	5.42	0.01
PC1+PC2+PC3+hatching date	110.26	5.83	0.01
PC2*PC3+hatching date	110.60	6.17	0.01

Appendix 5: Model set for the body mass of the nestlings; supported models are written in bold

variables involved in the models	AICc values	AICc difference	Akaike weights
PC3+PC2*PC4+date of hatching+nestling age+nr. of fledglings	**3849.71**	**0.00**	**0.37**
PC1+PC3+PC2*PC4+date of hatching+nestling age+nr. of fledglings	**3850.99**	**1.28**	**0.20**
PC2*PC3*PC4+date of hatching+nestling age+nr. of fledglings	3852.54	2.83	0.09
PC2*PC4+date of hatching+nestling age+nr. of fledglings	3853.71	4.00	0.05
PC1+PC2*PC4+date of hatching+nestling age+nr. of fledglings	3854.15	4.44	0.04
PC1*PC3+date of hatching+nestling age+nr. of fledglings	3854.97	5.26	0.03
PC2*PC3+date of hatching+nestling age+nr. of fledglings	3855.05	5.34	0.03
PC2+PC4+date of hatching+nestling age+nr. of fledglings	3855.20	5.49	0.02
PC2+PC3+PC4+date of hatching+nestling age+nr. of fledglings	3855.21	5.50	0.02
PC2+PC3+date of hatching+nestling age+nr. of fledglings	3855.24	5.53	0.02
PC1+PC2+PC4+date of hatching+nestling age+nr. of fledglings	3855.45	5.74	0.02
PC1+PC2+PC3+PC4+date of hatching+nestling age+nr. of fledglings	3855.92	6.21	0.02
PC3+date of hatching+nestling age+nr. of fledglings	3856.08	6.37	0.02
PC1+PC2+PC3+date of hatching+nestling age+nr. of fledglings	3856.45	6.74	0.01
PC2+date of hatching+nestling age+nr. of fledglings	3856.57	6.86	0.01
PC3+PC4+date of hatching+nestling age+nr. of fledglings	3857.26	7.55	0.01
PC1+PC2+date of hatching+nestling age+nr. of fledglings	3857.42	7.71	0.01
PC1*PC2*PC3*PC4+date of hatching+nestling age+nr. of fledglings	3857.51	7.81	0.01
PC1+PC3+date of hatching+nestling age+nr. of fledglings	3857.63	7.92	0.01
PC1+PC3+PC4+date of hatching+nestling age+nr. of fledglings	3858.65	8.94	0.00
PC3*PC4+date of hatching+nestling age+nr. of fledglings	3858.86	9.15	0.00
PC1*PC2+date of hatching+nestling age+nr. of fledglings	3859.10	9.39	0.00
date of hatching+nestling age+nr. of fledglings	3859.46	9.75	0.00
PC4+date of hatching+nestling age+nr. of fledglings	3859.73	10.02	0.00
PC1+date of hatching+nestling age+nr. of fledglings	3860.76	11.05	0.00
PC1+PC4+date of hatching+nestling age+nr. of fledglings	3860.77	11.06	0.00
PC1*PC4+date of hatching+nestling age+nr. of fledglings	3862.50	12.79	0.00

Appendix 6: Model set for the tarsus length of the nestlings; supported models are written in bold

variables involved in the models	AICc values	AICc difference	Akaike weights
PC3+date of hatching+nestling age+nr. of fledglings	**2162.57**	**0.00**	**0.24**
PC1+PC3+date of hatching+nestling age+nr. of fledglings	**2164.08**	**1.51**	**0.11**
PC2+PC3+date of hatching+nestling age+nr. of fledglings	**2164.14**	**1.57**	**0.11**
PC2*PC3+date of hatching+nestling age+gyuruzv e	**2164.48**	**1.91**	**0.09**
PC3+PC4+date of hatching+nestling age+nr. of fledglings	2164.63	2.06	0.08
PC1+PC2+PC3+date of hatching+nestling age+nr. of fledglings	2165.78	3.21	0.05
PC1*PC3+date of hatching+nestling age+nr. of fledglings	2165.90	3.32	0.04
PC1+PC3+PC4+date of hatching+nestling age+nr. of fledglings	2166.14	3.57	0.04
PC3*PC4+date of hatching+nestling age+nr. of fledglings	2166.17	3.60	0.04
PC2+PC3+PC4+date of hatching+nestling age+nr. of fledglings	2166.19	3.62	0.04
date of hatching+nestling age+nr. of fledglings	2166.39	3.82	0.04
PC2+date of hatching+nestling age+nr. of fledglings	2166.80	4.23	0.03
PC1+PC2+PC3+PC4+date of hatching+nestling age+nr. of fledglings	2167.84	5.27	0.02
PC1+date of hatching+nestling age+nr. of fledglings	2167.99	5.42	0.02
PC4+date of hatching+nestling age+nr. of fledglings	2168.27	5.70	0.01
PC2+PC4+date of hatching+nestling age+nr. of fledglings	2168.41	5.84	0.01
PC1+PC2+date of hatching+nestling age+nr. of fledglings	2168.58	6.01	0.01
PC2*PC4+date of hatching+nestling age+nr. of fledglings	2169.72	7.15	0.01
PC1+PC4+date of hatching+nestling age+nr. of fledglings	2169.92	7.35	0.01
PC1+PC2+PC4+date of hatching+nestling age+nr. of fledglings	2170.26	7.69	0.01
PC1*PC2+date of hatching+nestling age+nr. of fledglings	2170.31	7.74	0.00
PC1*PC4+date of hatching+nestling age+nr. of fledglings	2171.14	8.57	0.00

Appendix 7: Model set for the sex ratio at fledging age; supported models are written in bold

variables involved in the models	AICc value	AICc difference	Akaike weights
PC1+PC3+hatching date	**82.61**	**0.00**	**0.14**
PC1+PC2+PC3+hatching date	**83.03**	**0.42**	**0.11**
PC1*PC3+PC2+hatching date	**83.54**	**0.93**	**0.09**
PC3+hatching date	**83.81**	**1.20**	**0.08**
hatching date	**84.05**	**1.44**	**0.07**
PC1+hatching date	**84.20**	**1.59**	**0.06**
PC1+PC3+PC4+hatching date	**84.53**	**1.92**	**0.05**
PC1+PC2+PC3+PC4+hatching date	**84.56**	**1.95**	**0.05**
PC1*PC3+hatching date	**84.57**	**1.96**	**0.05**
PC2+PC3+hatching date	84.72	2.11	0.05
PC1*PC3+PC2+PC4+hatching date	85.28	2.67	0.04
PC2+hatching date	85.70	3.09	0.03
PC1+PC2+hatching date	85.81	3.20	0.03
PC3+PC4+hatching date	86.12	3.51	0.02
PC4+hatching date	86.24	3.63	0.02
PC1+PC4+hatching date	86.55	3.94	0.02
PC1*PC3+PC4+hatching date	86.70	4.09	0.02
PC2+PC3+PC4+hatching date	86.98	4.37	0.02
PC2*PC3+hatching date	87.07	4.46	0.01
PC3*PC4+hatching date	87.32	4.71	0.01
PC1*PC2+hatching date	87.81	5.20	0.01
PC2+PC4+hatching date	87.98	5.37	0.01
PC1+PC2+PC4+hatching date	88.27	5.66	0.01
PC1*PC4+hatching date	89.04	6.43	0.01
PC2*PC4+hatching date	90.51	7.90	0.00

Appendix 8: Model set for the body mass in connection with nestlings' sex; supported models are written in bold

variables involved in the models	AICc values	AICc difference	Akaike weights
date of hatching+nestling age+nr. of fledglings	**1473.29**	**0.00**	**0.27**
PC1*sex+date of hatching+nestling age+nr. of fledglings	**1473.45**	**0.16**	**0.25**
sex+date of hatching+nestling age+nr. of fledglings	**1475.02**	**1.73**	**0.11**
PC1*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1475.76	2.47	0.08
PC1*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	1476.16	2.88	0.06
PC4*sex+date of hatching+nestling age+nr. of fledglings	1476.53	3.24	0.05
PC1*sex+PC2*sex+date of hatching+nestling age+nr. of fledglings	1477.30	4.01	0.04
PC3*sex+date of hatching+nestling age+nr. of fledglings	1477.62	4.33	0.03
PC2*sex+date of hatching+nestling age+nr. of fledglings	1477.77	4.48	0.03
PC2*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1478.64	5.36	0.02
PC1*sex+PC2*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1478.91	5.63	0.02
PC1*sex+PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1479.18	5.89	0.01
PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1479.62	6.33	0.01
PC1*sex+PC2*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	1480.34	7.05	0.01
PC2*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	1480.92	7.63	0.01
PC2*sex+PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	1482.21	8.92	0.00
PC1+PC2+date of hatching+nestling age+nr. of fledglings	1482.89	9.61	0.00

Appendix 9: Model set for the tarsus length in connection with nestlings' sex; supported models are written in bold

variables involved in the models	AICc values	AICc difference	Akaike weights
date of hatching+nestling age+nr. of fledglings	**827.22**	**0.00**	**0.31**
sex+date of hatching+nestling age+nr. of fledglings	**827.43**	**0.21**	**0.28**
PC1*sex+date of hatching+nestling age+nr. of fledglings	**828.94**	**1.72**	**0.13**
PC3*sex+date of hatching+nestling age+nr. of fledglings	830.52	3.30	0.06
PC4*sex+date of hatching+nestling age+nr. of fledglings	830.53	3.31	0.06
PC2*sex+date of hatching+nestling age+nr. of fledglings	831.53	4.31	0.04
PC1*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	831.77	4.55	0.03
PC1*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	832.22	5.00	0.03
PC1*sex+PC2*sex+date of hatching+nestling age+nr. of fledglings	833.01	5.79	0.02
PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	834.25	7.03	0.01
PC2*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	834.58	7.36	0.01
PC2*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	834.66	7.44	0.01
PC1*sex+PC2*sex+PC3*sex+date of hatching+nestling age+nr. of fledglings	835.53	8.31	0.00
PC1*sex+PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	835.82	8.60	0.00
PC1*sex+PC2*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	836.39	9.17	0.00
PC2*sex+PC3*sex+PC4*sex+date of hatching+nestling age+nr. of fledglings	838.43	11.21	0.00
PC1+PC2+date of hatching+nestling age+nr. of fledglings	839.78	12.56	0.00

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Nyilatkozat

a szakdolgozatról

Alulírott

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című szakdolgozatom saját kutató munkám eredménye. Hozzájárulok, hogy a szerzői jogok tiszteletben tartása mellett a SZIE Állatorvos-tudományi Könyvtárban és az egyetemi adattárban elhelyezett nyomtatott és elektronikus példányokat az érdeklődők felhasználják az alábbi feltételekkel: (Kérjük aláhúzással jelölni)

Nyomtatott   másolható: részben / egészben

Elektronikus   megjeleníthető: belső hálózaton / szabad hozzáféréssel, interneten

_____
aláírás

Budapest, 2012. április 28.