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Effects of weather on breeding phenology of urban Eurasian kestrels *Falco tinnunculus*

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Abstract

Human-induced climate change and destruction of natural habitats are the two main threats to biodiversity worldwide. Animals can use weather conditions as environmental cues for optimal breeding conditions but climate change can cause severe phenological mismatches. Specifically migratory species that have a shorter time period for their settlement decision than residents, or species that breed in heavily transformed habitats – such as urbanised areas that can be linked to mismatches between perceived quality and realised fitness – might be sensitive to such changes. We analysed arrival and egg-laying dates of Eurasian kestrels (*Falco tinnunculus*) in Vienna (415 km^2), Austria, gathered by academic and citizen scientists from 2010-2018. To identify critical time windows in which weather variables affect egg-laying dates, we used a sliding window approach. We considered degree of urbanisation, observer category and year as additional co-variates. Furthermore, we assessed the relationship between arrival date and egg-laying (i.e., the length of the time gap in between). Egg-laying dates of urban Eurasian kestrels correlated significantly with precipitation prior to arrival until three weeks before egg-laying. We found that recorded arrival dates were influenced by observer category and year but not by urbanisation. Citizen scientists reported arrival and egg-laying dates earlier than academic scientists, while precipitation, daily maximum temperature and urbanisation were associated with later egg-laying dates. The time gap between arrival and egg-laying was shorter in breeding pairs that arrived later at their nest sites. We conclude that in our case degree of urbanisation, observer category and precipitation are the most important factors to understand breeding phenology, although the inter-annual variation was high. Temperature featured significantly in the models but naturally increased over the course of the breeding period and thus is confound with a seasonal effect. Our results indicate a strategy to mitigate later arrival by relatively earlier egg-laying through reducing the courtship period. This suggests a behavioural adaption to take advantage of potentially favourable conditions at the wintering grounds while avoiding egg-laying delay and the associated declines in breeding productivity with later onset of breeding known also from previous studies in our population.

Introduction

Human-induced climate change and destruction of natural habitats threaten global biodiversity greatly, posing new challenges throughout all habitats and from species to community level (Hendry et al., 2017; Parmesan, 2006; Pimm & Raven, 2000; Root et al., 2003; Secretariat of the Convention on Biological Diversity, 2006; Walther et al., 2002). Due to the continuous growth of human population and associated resource use (Vitousek, 1994), both climate and land-use change are expected to intensify further within this century (Sala et al., 2000). In fact, the United Nations Secretariat considers climate change and land-use change in form of urbanisation to be one of the most significant current sources of global environmental change (United Nations, 2019). Globally, more than half of the human population is urban dwelling by today, which is expected to extend to 70% until 2050 (Grimm et al., 2008; Roberts, 2011). In Europe, urbanisation is one of the most fundamental characteristics of civilisation (Antrop, 2004); so in 2018 74% of the human population lived in urban areas and their surroundings (United Nations, 2019).

One key mechanism induced by global change is the phenological shift, i.e. an altered timing of seasonal life cycle activities or events (Walther et al., 2002; based on Lieth, 1970). These shifts might be caused by changing abiotic factors, for instance snow melt affecting flowering of plants (Inouye, 2008), but also entail biotic interactions (Miller-Rushing et al., 2010). However, phenological shifts can be positive or negative. For example, earlier springs and longer frost-free seasons with reduced snowfall advance flowering of plants and egg-laying in birds (Zohner, 2019), which might promote exploitation of newly available resources (Miller-Rushing et al., 2010) with associated fitness advantages. On the other hand, such shifts can cause temporal mismatches within trophic levels, e.g. between plants and pollinators or predators and prey (Both et al., 2009; Edwards & Richardson, 2004; Renner & Zohner, 2018; Stenseth & Mysterud, 2002; Visser & Both, 2005; Visser et al., 2006). In urban surroundings, phenological shifts could be enhanced by the urban heat island effect (Arnfield, 2003; Oke, 1982; Streutker, 2003).

Seasonality of the environment restricts time windows suitable for reproduction or growth of plant and animal species (Visser & Both, 2005). For breeding birds, the question when and where to breed determines their own and their offspring's fitness (Daan & Tinbergen, 1997). Although birds are highly mobile, they are inherently dependent on their surrounding environment as soon as they start breeding. To enhance reproductive productivity, birds need to time the hatching of their young as close to the environmental optimum as possible but initiate the breeding process well before this environmental

optimum occurs (Daan et al., 1989; Perrins, 1970). Consequently, predictions of ideal conditions – especially the sufficient availability of suitable food to raise offspring – is based on environmental cues at the time before breeding (Baker, 1938; Murton & Westwood, 1977; Wingfield, 1983). The long-term predictors for breeding birds of temperate zones are photoperiodical cues (see review Sharp, 1996). But the longer the time gap between the perception of the cue(s) and the fitness consequences, the higher the probability of mismatches (Padilla & Adolph, 1996). This becomes even more challenging in a severely changed environment, such as core urban areas, where cue mismatches can also happen through anthropogenic influences. Species face severely different environmental conditions in altered systems than they experienced in the fitness landscape they evolved in (Tilman & Lehman, 2001).

To adjust the fine-tuning to local conditions, additional factors closer to the actual onset of breeding might be important predictors for breeding (Visser et al., 2010), especially spring temperatures (i.e. less than one month before egg-laying; see review Williams et al., 2015). Getting the timing right matters, because earlier clutches have a higher chance of survival and offspring of earlier broods are more likely to recruit into the breeding population (Grüebler & Naef-Daenzer, 2010; Harriman et al., 2017; Perrins, 1970; Verboven & Visser, 1998). Furthermore, Perrins (1970) hypothesised, that the onset of breeding is limited by the fitness of the parents, e.g. by food supply for the female to reach breeding condition (Drent & Daan, 1980). The fitness advantage of earlier hatched young can be attributed to environmental quality deteriorating throughout the season, thus making timing *per se* the main driver of fitness loss ('date hypothesis', Perrins, 1970; see reviews Harriman et al., 2017; Verhulst & Nilsson, 2008). Additionally, the high phenotypic plasticity of the parents in form of their higher age (e.g. Daunt et al. 1999; Forslund and Pärt 1995), better body condition (e.g. Chastel et al., 1995; Kokko 1999; Perrins 1970) or high quality of territories occupied earlier in the season (e.g. Sergio et al. 2007) could yield fitness benefits ('quality hypothesis', within the Ideal Dominance Distribution or Ideal Despotic Distribution (Fretwell, 1972)). Both hypotheses are not necessarily mutually exclusive, especially if parents face an optimization process in which they trade-off breeding benefits (which might be related to the date hypothesis) and fitness costs (which might related to the quality hypothesis) associated with breeding time (Grüebler & Naef-Daenzer, 2010; Verhulst & Nilsson, 2008). Similarly, earlier-arriving individuals in migratory species are usually fitter than later-arriving ones, and settle on progressively lower-quality territories (Sergio et al., 2007). Early arrival may therefore be advantageous in terms of higher reproductive performance.

Human-induced rapid environmental change (HIREC; Sih, 2013), such as climate and land-use change, have severely altered the phenology of birds and numerous other organisms,

consequently influencing their reproduction and population viability (Jetz et al., 2007; Møller et al., 2008; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Visser et al., 2012; Walther et al., 2002). Large-scale land-cover changes can have detrimental effects on species either through habitat loss and fragmentation (Huhta & Jokimäki, 2008; Newbold et al., 2015) or by uncoupling cues used to select a suitable habitat and the true value of this habitat (Battin, 2004). Such misinterpretation of habitat is known as ecological trap (see review Battin, 2004; Dwernychuk & Boag, 1972; Kokko & Sutherland, 2001; Kristan, 2003; Robertson & Hutto, 2006; Schlaepfer et al., 2002). Urbanisation potentially endangers more species than any other human activity or land-use change (Czech et al., 2000). It is associated with decreasing species richness, diversity and changes in species composition (see review Blair, 1996; McKinney, 2002). Physical changes, reaching from increases in pollution, average ambient temperature, soil compaction and alkalinity, to increased unproductive surface (sealed soil) and less space (high human population density), cause declines in biodiversity (Sol et al., 2014). However, the total density of birds is often maintained by urban exploiters and adaptors profiting from available food resources, enhanced availability of nesting sites (e.g. cavity breeders), predator reduction and reduced human persecution (Lancaster & Rees, 1979; Marzluff, 2001; McKinney, 2002).

One species that appears intrinsically resilient to urbanisation and even proliferates in human-modified environments is the Eurasian kestrel *Falco tinnunculus* (hereafter 'kestrel'). In this study we analyse long-term data on arrival from wintering grounds and the timing of breeding (2010-2018) from the kestrel population in Vienna, Austria. The kestrel is the most common raptor species of the Palearctic region and Vienna holds the highest density of non-colonially urban breeding individuals (Sumasgutner et al., 2013; Wichmann et al., 2009). In natural areas kestrels mainly breed in deserted or usurped corvid nests or in cliff cavities (Village, 1990), but they opportunistically use anthropogenic structures available in urban settings (Kübler et al., 2005; Sumasgutner, Nemeth, et al., 2014; Sumasgutner, Schulze, et al., 2014; Village, 1990). If voles, which are the kestrel's main prey, decline in availability due to natural cycles (Korpimäki, 1986; Valkama et al., 1995) or become less available due to urbanisation (Sumasgutner, Nemeth, et al., 2014), kestrels adjust by broadening their diet width and hunting habitat (Korpimäki, 1986; Kreiderits et al., 2016; Kübler et al., 2005; Mikula et al., 2013; Sumasgutner et al., 2013; Valkama et al., 1995) and by increasing hunting effort and enlarging hunting areas (Riegert, Dufek, et al., 2007; Riegert, Fainová, et al., 2007). Consequentially, there is a strong implication that kestrels are urban adaptors. Nevertheless, it is yet unclear if core urban areas impose an ecological trap for this raptor species. Inner-city habitats are readily accepted by the kestrels but are associated with reduced prey availability,

breeding productivity and offspring's individual health (Sumasgutner et al., 2018; Sumasgutner, Nemeth, et al., 2014). Adults breeding in urban core areas are likely to be affected by these concomitant fitness costs, too.

Previous studies showed that weather parameters during winter, arrival and courtship affect breeding productivity of kestrels in Vienna, in a way that higher spring rainfall reduces productivity, probably due to delayed egg-laying (Kreiderits et al., 2016). In Mediterranean kestrels dry and mild winters reduce breeding productivity, but at the same time higher spring rainfall delays egg-laying dates (Costantini et al., 2010b), indicating that different breeding stages are sensitive to different time-windows. Thus, it remains a worthy endeavour to identify which weather predictors are the most relevant during which periods. These critical time windows might act as additional cues to photoperiodism, which has a significant effect on the reproduction of kestrels in general and explains variation of egg-laying dates in the Western Palearctic (Carrillo & González-Dávila, 2009; Meijer et al., 1992). However, if this is the sole predictor, variation in response to global change would be heavily limited.

In this study we aim to first (i) determine the start, duration and key variables of the critical time window(s) which predict egg-laying dates of kestrels in Vienna. We expected the critical time window(s) to coincide with the winter before breeding, arrival and courtship period. This could be evident in either (a) several shorter critical time windows, or (b) one long critical time window starting before arrival and ending during courtship. We furthermore expected precipitation to be the strongest predictor with a larger effect in rural compared to urban nest-sites as buildings might provide better cover. A similar assessment of the arrival time at the nest-site after migration was not possible due to the lack of information where kestrels of the investigated population overwinter.

Second (ii), we are interested if the onset of breeding is determined by the arrival time itself. This would be the case if courtship duration (time gap from arrival until egg-laying) stays constant from early to late arrivals. Alternatively, egg-laying could be relatively earlier (shortening time gap) or later (elongating time gap), suggesting more independent mechanisms that determine arrival time after migration and timing of breeding. Shortening of time gaps could indicate a strategy of mediating later arrival (and thus avoiding potential related fitness costs of living in urban environments for the parents) by relatively earlier onset of breeding. Contrary, elongating time gaps could indicate cascade effects within fitness costs of late broods, as late arrivals lead to even later broods. Furthermore, these time gaps could vary depending on the degree of urbanisation. For example, a shorter time gap at urban nest-sites would indicate that the females reach breeding condition earlier in an urban setting, and *vice versa,* a longer time

gap at urban nest-sites would indicate that the females reach breeding condition later in an urban setting.

Third (iii), due to the high involvement of the general public into the monitoring program and the profound integration of data originating from citizen scientists, we want to understand the influence of observer category (academic scientists vs. citizen scientists), the quality of the provided information and potential effects of urbanisation on availability of citizen scientists. Citizen science has become an increasingly used research tool and particularly popular in ornithology and migration phenology (Bonney et al., 2009; Cooper et al., 2014) but should be used mindfully and with clarity (Bonney et al., 2009; Burgess et al., 2017; Cooper et al., 2014).

Our final objective was to build a global model to predict arrival time and egg-laying dates based on the insights gained from (i) – (iii) to gain a deeper understanding of the ecological processes shaping the population dynamics of kestrels along an urbanisation gradient.

Material and Methods

Study species

The kestrel population of Vienna ranges between 89 – 122 breeding pairs/100km^2 (Sumasgutner, Schulze, et al., 2014) and is monitored systematically since 2010 ('Turmfalkenprojekt Wien'). Kestrels are considered partial migrants, but the redistribution of kestrels in post-breeding migrations varies immensely with latitude (Village, 1990). It is yet unclear where the kestrel population of Vienna is migrating to. Unlike populations studied in other European cities, kestrels in Vienna disperse in mid-summer and temporarily leave the city during winter (Riegert & Fuchs, 2011; Romanowski, 1996; Sumasgutner, Nemeth, et al., 2014). Only few, primarily male individuals are known to spend the winter within urban areas of Vienna (Adrion, 2016). Within Europe, females and juveniles travel larger distances than males and adults (Terraube et al., 2015), whereby post-breeding migration starts in September/October and is preceded by dispersal movements in August (Holte et al., 2016). In early spring, the kestrels return to Vienna (Sumasgutner, Nemeth, et al., 2014). In 2010 and 2011, inner-city territories were occupied slightly before territories in areas with less sealed area, indicating a preference for inner-city nest sites (Sumasgutner, Nemeth, et al., 2014).

In contrast to their conspecifics in suburban and natural habitats who mainly feed on voles, the urban kestrel's prey composition is more diverse and largely based on alternative prey species such as other small mammals, passerine birds and swifts, reptiles,
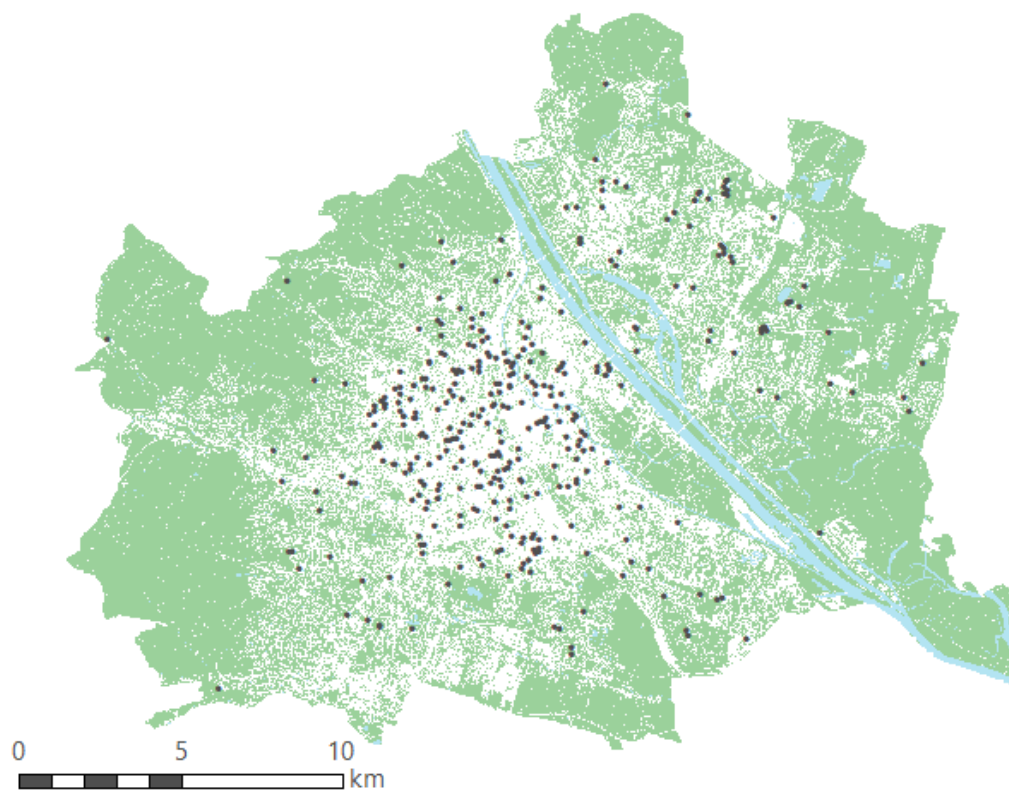
Fig. 1: Location of all nest sites (n = 366) observed between 2010 and 2018 in Vienna, Austria (marked as grey points). Water bodies are displayed in blue, unsealed surfaces in green, impervious surfaces in white.

and insects (Kreiderits et al., 2016; Kübler et al., 2005; Mikula et al., 2013; Sumasgutner et al., 2013). The kestrel density of Vienna is relatively high compared to other European cities and rural surroundings (Gamauf, 1991; Kostrzewa & Kostrzewa, 1993; Sumasgutner, Nemeth, et al., 2014)

Study area and urbanisation gradient

Vienna (48°12′N, 16°22′E, 150-500 m.a.s.l., 415 km^2, 1.88 million inhabitants), the capital of Austria, is considered a 'green' city with approximately 50 % of the total area being green areas (Municipal Department 23 - Economy, 2018) including urban green space but also agricultural, forest and conservation areas located within the cities' boundaries.

We quantified a soil seal factor (SSF) as percentage of impervious surfaces within a buffer circle of r = 500 m (78.5 ha) around each nest site, corresponding to the lower end of kestrel hunting area sizes reported from Kiel, Germany (range of 90-310 ha; Beichle, 1980) and České Budějovice, Czech Republic (range of 80-2500 ha; Riegert, Fainová, et al., 2007). We chose the smaller scale because of the high breeding density of kestrels in Vienna, as high densities usually correlate to smaller home range sizes in urban raptors (e.g. Dykstra

et al., 2001; Dykstra et al., 2018; Rutz, 2006). The SSF was our proxy for an urbanisation gradient and excluded rural areas, defined as areas with SSF < 1%, thus limiting the study area to 243 km^2.

The SSF was calculated using ArcMap (ESRI Inc., 2017) from land allocation maps provided by the Environmental Protection Bureau of Vienna (MA 22 – Umwelt). These maps indicated 51 different land cover categories, which were aggregated into impervious and unsealed surfaces (Fig. 1; Supplement, Tab. I). 35 land cover categories, such as buildings, roadways, pavements or parking lots, were assumed to be impervious. The remaining 16 land cover categories like unsealed yards, grasslands, forests, agricultural areas, wine yards, cemeteries, gravel pits and various sorts of water bodies were classified as unsealed soil. Since the land allocation maps are renewed within periods of four years, the SSF was calculated based on one map that was digitised between 2010 and 2013 for all nest sites occupied before 2014 and on a map that was digitised between 2014 and 2017 for all other nest sites. Thus, some nest sites which were occupied by kestrels in both time periods were attributed with two different SSFs respective to the year observed. The SSF of all observed nest sites ranged from 4.77 % to 98.52 %.

The monitoring program

The monitoring of the Viennese kestrel population started in 2010 and incorporated systematic observations by academic scientists, data contributed by ornithologists involved in the breeding-bird survey and citizen science data reported by phone, e-mail, social media or via BirdLife Austria and the online platform bird.at. Data was obtained from all over Vienna (Fig. 1).

The contribution of each citizen varied strongly in extent and quality. While plenty of citizens did not report observations repeatedly, various contributors became a distinctive part of the project, reliably reporting on the arrival and reproduction at "their" nest site season after season. Often comprehensive pictures of the brood were provided. All reports were documented and notifications of (yet) unknown contributors without any supporting footage were verified *in situ* by academic scientists. Nevertheless, previous studies mostly focused on less nest sites than overall reported as they relied on nest sites accessible for direct manipulation such as measuring, weighing, and banding the nestlings. Therefore, no standardised procedure for validation of data provided by citizen scientists has been introduced up to now.

The following analyses includes all data reported from 2010 to 2018 by academic and citizen scientists. Arrival and egg-laying dates were extracted from the notes taken by field scientists and, if necessary, backed up by re-vising written communication with

contributing citizens. Several citizen scientists stated when they first observed the kestrels at the nest after the non-breeding season. As kestrels show very prominent behaviour at the nest site, we assumed the time gap between arrival at the nest site and first notice by the citizens to be quite short. In case no specific arrival date was reported, the first date of correspondence of the citizen scientists was used as a substitute.

Several nest sites in Vienna offer a direct view from buildings located vis-à-vis, facilitating nest controls without nest disturbance. Nesting in flowering boxes on windowsills easily allow for daily nest controls, too. However, several nest sites cannot be seen from a vantage point and can only be accessed via attics, by climbing trees or with the help of the Vienna Fire Fighters and the Vienna Chimney Sweepers, who supported the monitoring program since its very beginning. Observations from the ground can give relevant cues on reproduction phenology but cannot be as precise as direct nest controls. Therefore, in seven of nine years of the monitoring program, nestlings of accessible nests were at least once examined, measured and ringed. As part of the examination, the age of the nestlings could be estimated via morphometric measurements, allowing a back-dating of the hatching and egg-laying dates (Kostrzewa & Kostrzewa, 1993). Therefore, egg-laying date was either observed directly, or deduced by calculating 30 days back from the hatching date (Village, 1990). The project field notes specified if observations on the breeding stage were based on direct assessment or by reports of citizens. In cases were no such details were provided, we went back into e-mail and social media conversations where possible. Only in a few cases it was not possible to determine where the information originated from.

Another important step was to carefully consolidate the data between years. As no central database was used to administer and maintain all observations of nest sites from the beginning, nest IDs and locations were double checked before joined into one database.

Weather data

Weather data on temperature and precipitation was obtained from the Central Institute for Meteorology and Geodynamics (ZAMG) as well as the Tutiempo Network, S.L. Both provide data from the weather station 'Vienna inner-city', which is located in the 4th district of Vienna, 1.3 km from the centre of the city. Four different weather variables were analysed separately: daily (24h) average temperature (T_{ave} given in °C), maximum temperature (T_{max} given in °C), minimum temperature (T_{min} given in °C) and total precipitation (PP, given in mm).

Statistical analysis

All statistical analyses were performed in R 3.6.1 (R Core Team, 2019). Confidence intervals were set to 95 % and significance is referred to as p ≤ 0.05 %. Arrival and egg-laying dates were processed as Julian days and were normally distributed. Of all recorded arrival dates, dates before the 1st of February and after the 21st of June were excluded (n = 11, mainly before the 1st of February). The dates before 1st of February were likely to stem from males wintering in Vienna. The dates after 21st of June were rare statistical outliers, which are likely to result from relocations after nesting failure.

In 2013 and 2018, the monitoring was conducted less systematically compared to the other years. Thus, data from these years were excluded from the model on arrival dates (n = 3 each), leaving 515 observations to be analysed. For egg-laying dates, years 2016 and 2018 were excluded ($n_{2016} = 0$, $n_{2018} = 6$) as no banding (with age-assessment of the offspring) took place, leaving n= 114 observations to be analysed.

Additionally, arrival and egg-laying dates were documented at the same nest and within the same year in 68 cases, thus allowing for exact assessment of the time gap between arrival and egg-laying (Δ Days). These observations (hereafter 'corresponding observations') were obtained irregularly in the years 2010-2012, 2014-2015, and 2017-2018.

To test hypothesis (i) and determine time windows during which weather variables affect egg-laying dates (and hence, kestrels are sensitive to weather conditions), we followed a sliding window approach (Brommer et al., 2008; Williams et al., 2015). For this purpose, multiple Pearson's correlations were calculated for the annual mean egg-laying dates and the average of weather variables for various alternative time windows (Fig. 2). We chose the length to vary between 1-90 days and tested every possible time window within a period starting 90 days before the mean annual laying date (n = 29295). We performed the sliding window approach for each weather variable separately and calculated R^2 values from the Pearson's correlations. When daily values for weather variables were missing (N.A.), they were removed from analyses. If a time frame consisted of N.A.s exclusively, no result was calculated.

For the testing if (ii) the onset of breeding was already determined by the arrival time itself, we used the data set of corresponding observations mentioned above and performed a linear regression with ΔDays as dependent variable and arrival date as independent variable, using the lm() command in the *base* package (R Core Team, 2019).

To assess (iii) if any observer effects (academic vs. citizen scientists) caused variation in the reported dates and to find global models to predict arrival and egg-laying dates, we calculated linear mixed-effect models (LMMs) via maximum likelihood with a Gaussian error distribution. We integrated nest ID (as random term), year of observation (as fixed
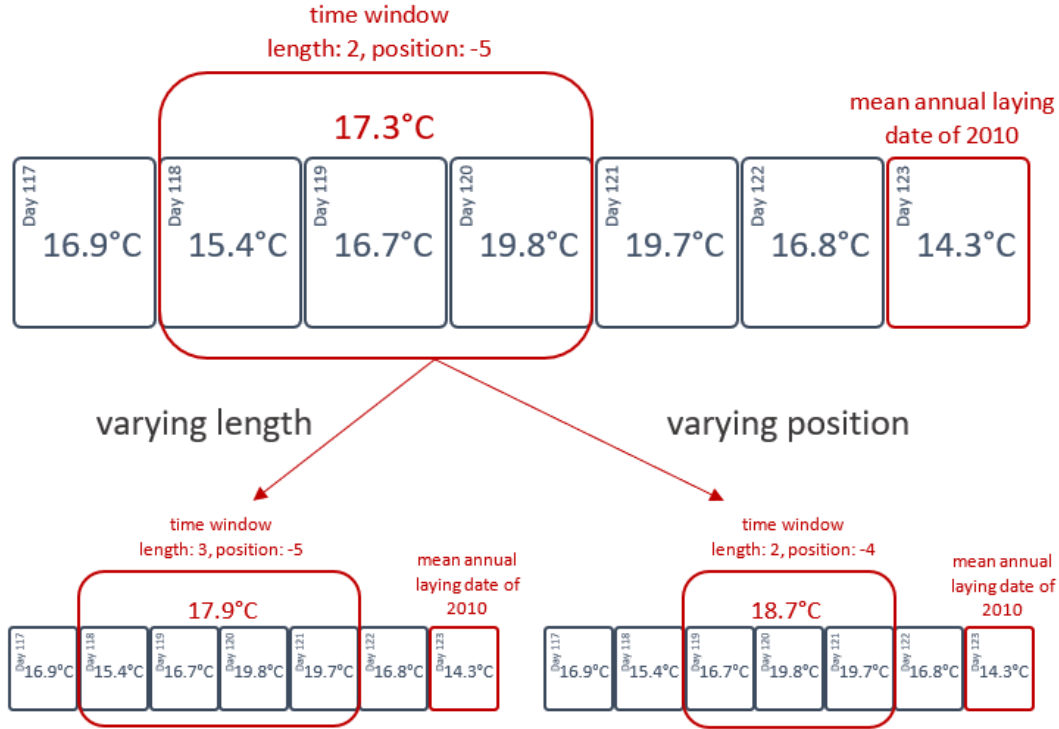
Fig. 2: Illustration of the sliding window approach in 2010 for the daily average temperature. Each time window is defined by its length (in nights, therefore 0 includes 24h) and position (starting point in days, with the mean annual laying date being day 0).

effect or random term), observer category (as fixed effect) and SSF (as fixed effect). The year was tested as random term and as fixed effect to account for yearly variation in the remaining independent variables. For the model on egg-laying dates, we integrated the two most informative weather variables within the optimal time window assessed in (i). The arrival date was considered as a fixed effect when working with the data set of corresponding observations.

All LMMs were built with lmer() in the package *lme4* (Bates et al., 2015). Additionally, the packages *LMERConvenienceFunction* (Tremblay & Ransijn, 2015) and *car* (Fox & Weisberg, 2019) were used for model validation by inspection of residuals. AIC() in the *base* package (R Core Team, 2019) was applied to choose between the models concerning the status of the year of the observation (random term or fixed effect). The conditional R^2-values (hereafter 'R^2LMMc'; Nakagawa et al., 2017) of the models were calculated with r.squaredGLMM() of the *MuMIn* package (Barton, 2019); significance of explanatory terms were assessed using their partial (Type III) significance values (χ^2-tests).

For data visualisation, the additional packages *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2019) were used. Effect plots were made using the package *lattice* (Sarkar, 2008).

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Results

Time windows and weather variables affecting egg-laying date

Precipitation (PP) and maximum daily temperature (T_{max}) proved to be the most informative weather variables with the highest explanatory capacity (Fig. 3), while average daily temperature (T_{ave}) was ranked second and daily minimum temperature (T_{min}) appeared to be least informative (Supplement, Fig II).

For PP, we found several, partly overlapping critical time windows. Two patterns could be derived from the critical time windows (Fig. 3). First, time windows incorporating data from the last three weeks before mean egg-laying showed little explanatory capacity, whilst windows ending about 20 days before the mean annual laying date scored high R^2-values (> 0.5) but varied in position and length. Second, time windows of more than three weeks length which started from around 80 days (2.5 months) before egg-laying were more informative, displaying R^2-values > 0.5. Highest R^2-values were recorded where the time windows of the two patterns were identical, with the maximum R^2 = .82 associated to a time window of length = 58 and position = -79, thus starting 79 days (approx. 11 weeks) and ending 21 days (3 weeks) before the egg-laying. Within this time window, PP was positively correlated with later egg-laying date.

For T_{max}, fewer critical time windows and less patterns were found compared to PP (Fig. 3). Time windows of about 20 days that started approximately one month before egg-laying were most informative. The maximum R^2 = 0.82 was assigned to a time window of length = 20 and position = -40 (i.e., the time window started 40 days and ended 20 days before egg-laying). During this time window, T_{max} was negatively correlated with later egg-laying date. Among the other weather variables T_{min} scored the lowest R^2-values (max. R^2 = 0.63). T_{ave} reached its maximum informative value R^2 = 0.71. All temperature parameters (T_{min}, T_{max}, T_{ave}) were highly correlated with each other ($T_{min} - T_{max}$: $r_{(1258)}$ = 0.93; P < 0.001. $T_{min} - T_{ave}$: $r_{(1258)}$ = 0.97; P < 0.001. $T_{max} - T_{ave}$: $r_{(1258)}$ = 0.98; P < 0.001).
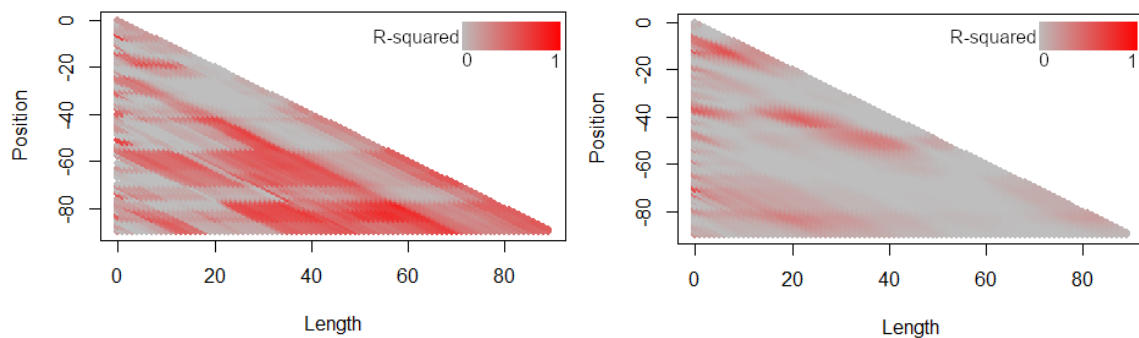

Fig. 3: Depiction of R^2-values derived by the sliding window approach on precipitation (PP, left) and daily maximum temperature (T_{max}, right). Both show a maximum R^2 = 0.82: PP at length = 58 and position = -79 (approx. 11 to 3 weeks before egg-laying), T_{max} at length = 20 and position = -40 (approx. 6 to 3 weeks before egg-laying).

Dependency of egg-laying on arrival date

The time gap between arrival and egg-laying date (ΔDays) for corresponding observations (n = 68) decreased for later arrival dates (Fig. 4; $F_{(1,66)}$ = 26.47; $P < 0.001$; R^2 = 0.28; estimate = -0.55), which means egg-laying started relatively earlier with corresponding later arrival date. ΔDays decreased by approximately half a day per later day of arrival.
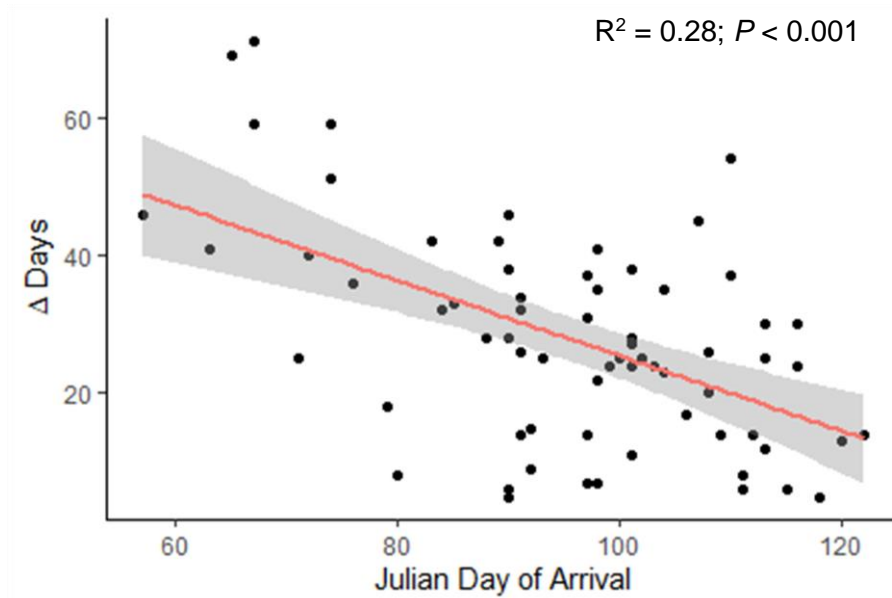
Fig. 4: The time gap between arrival and egg-laying date (ΔDays) decreases for later arrival dates when pooling corresponding observations from all years (n = 68).

Observer effects

Between 2010 and 2018, citizen scientists reported more arrival but less egg-laying dates than academic scientists (Tab. 1, Fig. 5). Observer category significantly affected both arrival date ($\chi^2_{(1, 513)}$ = 3.95; P = 0.047) and egg-laying date ($\chi^2_{(1, 209)}$ = 7.14; P = 0.008; Tab. 2). The mean arrival date determined by citizen scientists was day 97.1 ± 15.1 (7th of April), whereas the mean arrival date ascertained by academic scientists was day 103.2 ± 12.9 (13th of April). Thus, citizen scientists reported arrivals on average one week in advance (Fig. 6). The mean egg-laying date reported was day 122.4 ± 19.2 (2nd of May) for citizen scientists and day 123.8 ±14.2 (4th of May) for academic scientists.

Tab. 1: Sample size of arrival and egg-laying observations in relation to the observer category.

	Academic Scientist	Citizen Scientist
Arrival date	194	319
Egg-laying date	179	30
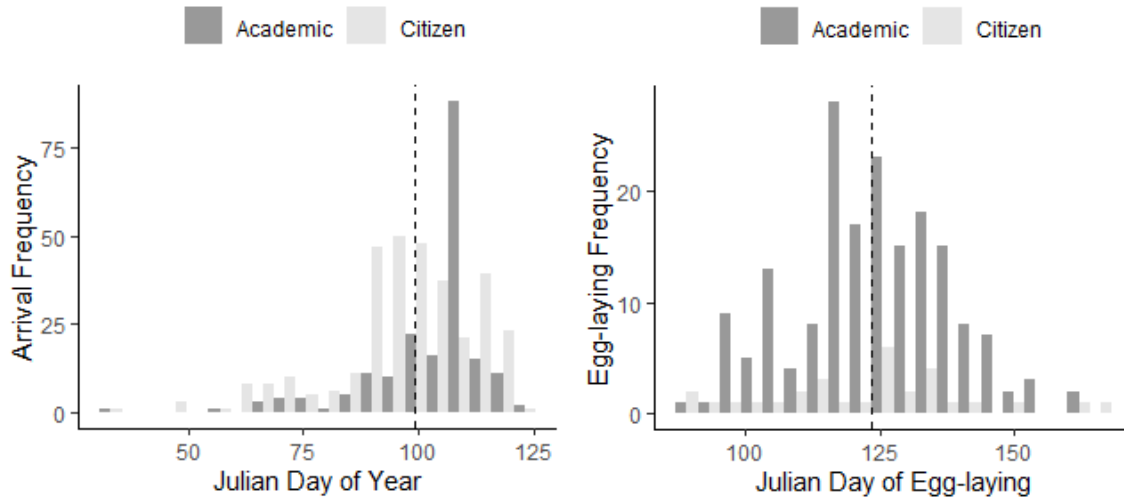
Fig. 5: Citizen scientists reported more arrivals at the nest sites (in total n = 521; left), whereas academic scientists reported more egg-laying dates (in total n = 220; right).
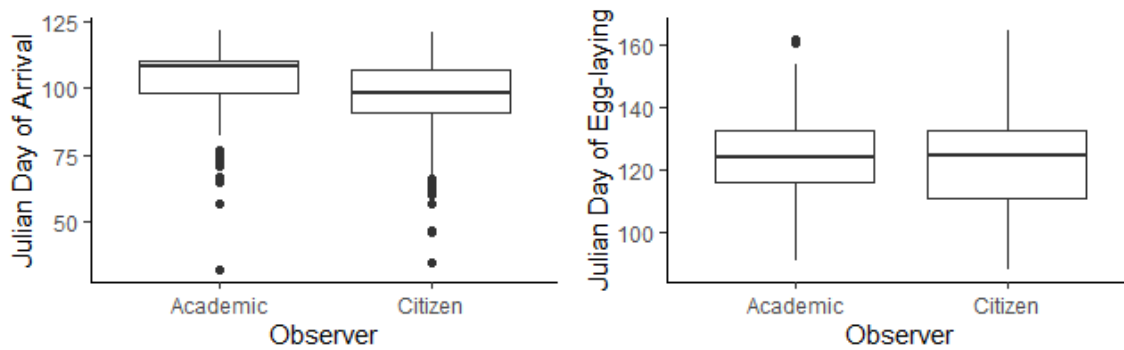
Fig. 6: Citizen scientists reported the arrival at the nest 7 days in advance to academic scientists. No such difference was found for egg-laying dates.

Linear Mixed Models

For arrival dates, we fitted two competing models. Both included SSF and observer category as fixed effects and nest ID as random term. The year of the observation was either incorporated as fixed effect (model 1) or as random term (model 2). After inspection of AIC values ($AIC_{model\,1}$ = 4102.58; $AIC_{model\,2}$ = 4128.81), model 1 was chosen as final model on arrival dates (Tab. 2; Fig. 7; R^2LMMc = 0.21). Year ($\chi^2_{(6,\,515)}$ = 27.94; $P < 0.001$) and observer category ($\chi^2_{(1,\,513)}$ = 3.95; $P = 0.047$) were significant (Fig. 7). The estimates on arrival dates varied from 6.24 to -4.50 days between years, with the earliest reports in 2017 and the latest in 2011. Academic scientists reported arrivals on average 3.49 days later. SSF was not significant ($\chi^2_{(1,\,509)}$ = 1.36; $P = 0.243$).

Likewise, we fitted two competing models on egg-laying dates. There was no co-linearity between precipitation (PP) and daily maximum temperature (T_{max}) within the critical time windows ($r_{(209)}$ = 0.12; $P = 0.062$) so both were fitted into the same models. SSF and observer category were additional co-variates and nest ID was fitted as random term.

Tab. 2: LMMs on arrival dates (years 2010-2012, 2014-2017) and egg-laying dates (years 2010-2015 and 2017), exploring the effects of Soil Seal Factor (SSF), observer category (academic vs. citizen scientist), year and, in the final model on egg-laying dates, precipitation (PP, daily precipitation mean from 21-79 days before egg-laying) and maximum temperature (T_{max}, daily maximum temperature mean from 20-40 days before egg-laying).

	Estimate	SE	χ^2	P	Sign.	R^2LMMc
Arrival date ~ SSF + Observer + Year + (1 | nest ID)						0.21
SSF	-0.04	0.03	1.36	0.243	-	
Observer‡			3.95	0.047	*	
Academic scientist	3.49	1.76				
Year†			27.94	< 0.001	***	
2011	6.24	1.92				
2012	5.55	3.75				
2014	0.73	2.60				
2015	5.64	2.50				
2016	3.92	3.98				
2017	-4.50	2.53				
Intercept	98.74	2.57	1476.05	< 0.001	***	
Egg-laying date ~ PP + T_{max} + SSF + Observer + Year + (1 | nest ID)						0.77
PP	23.47	1.98	140.29	< 0.001	***	
T_{max}	2.62	0.17	239.74	< 0.001	***	
SSF	0.05	0.02	4.03	0.045	*	
Observer‡			7.14	0.008	**	
Academic scientist	4.33	1.62				
Year†			60.10	< 0.001	***	
2011	1.25	2.09				
2012	1.97	1.88				
2013	11.01	2.13				
2014	-4.69	2.11				
2015	-0.45	2.09				
2017	-1.13	2.49				
Intercept	50.59	3.74	182.78	< 0.001	***	

‡ observer 'citizen scientist' and † Year 2010 were used as reference categories; significance categories were set as '***' = P < 0.001; '**' = P < 0.01; '*' = P < 0.05.
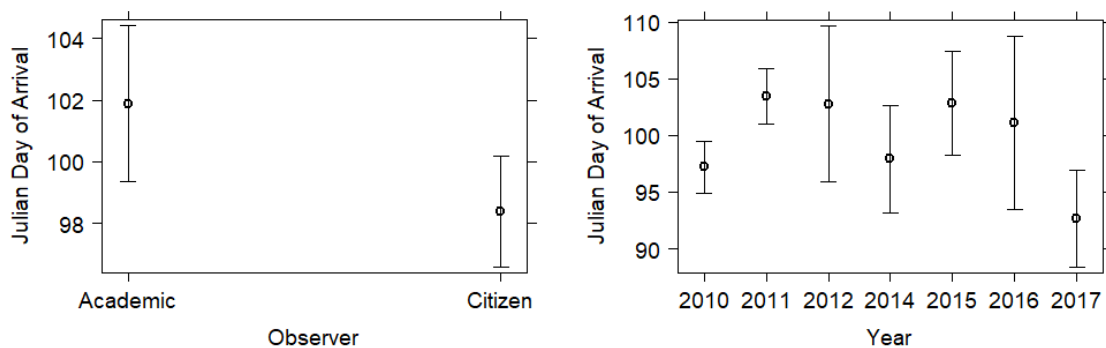

Fig. 7: The LMM on arrival dates featured observer category and study year as significant explanatory terms. The overall R^2c of the LMM was 0.21. Model details in Table 2.

Model 1 with year as fixed effect (Tab. 2; Fig 8; R^2LMMc = 0.77) was chosen as final model on egg-laying dates (AIC$_{model\ 1}$ = 1369.21; AIC$_{model\ 2}$ = 1397.08). Significant explanatory terms were PP ($\chi^2_{(1,\ 211)}$ = 140.29; $P < 0.001$), T_{max} ($\chi^2_{(1,\ 211)}$ = 239.74; $P < 0.001$), SSF ($\chi^2_{(1,\ 206)}$ = 4.03; $P = 0.045$), observer category ($\chi^2_{(1,\ 209)}$ = 7.14; $P = 0.008$) and year ($\chi^2_{(6,\ 211)}$ = 60.10; $P < 0.001$). While year had an ambivalent effect, observations by academic scientists and higher PP, T_{max} and SSF were positively correlated with later egg-laying dates (Fig. 8).

An additional LMM was performed using the smaller data set of corresponding observations which provided arrival and egg-laying dates from the same nest and breeding season. Weather variables, arrival date and SSF were fitted as fixed effects and nest ID as random term, year was as before tested as fixed effect and random term. Observer category could not be included as the respective events were not necessarily reported by the same observer.

Here, too, the final model included year as fixed effects (model 1; AIC$_{model\ 1}$ = 403.27; AIC$_{model\ 2}$ = 428.55; Tab. 3; Fig. 9). PP ($\chi^2_{(1,\ 68)}$ = 79.78; $P < 0.001$), T_{max} ($\chi^2_{(1,\ 68)}$ = 56.78; $P < 0.001$), year ($\chi^2_{(6,\ 68)}$ = 18.34; $P = 0.005$) and arrival date ($\chi^2_{(1,\ 68)}$ = 6.16; $P = 0.013$) were significant fixed effects. SSF was not significant ($\chi^2_{(1,\ 65)}$ = 0.41; $P = 0.523$). This model featured the highest R^2LMMc = 0.85.

All models showed acceptable QQ-plots and bell curves when inspecting the residuals (Supplement, Fig. III – V)
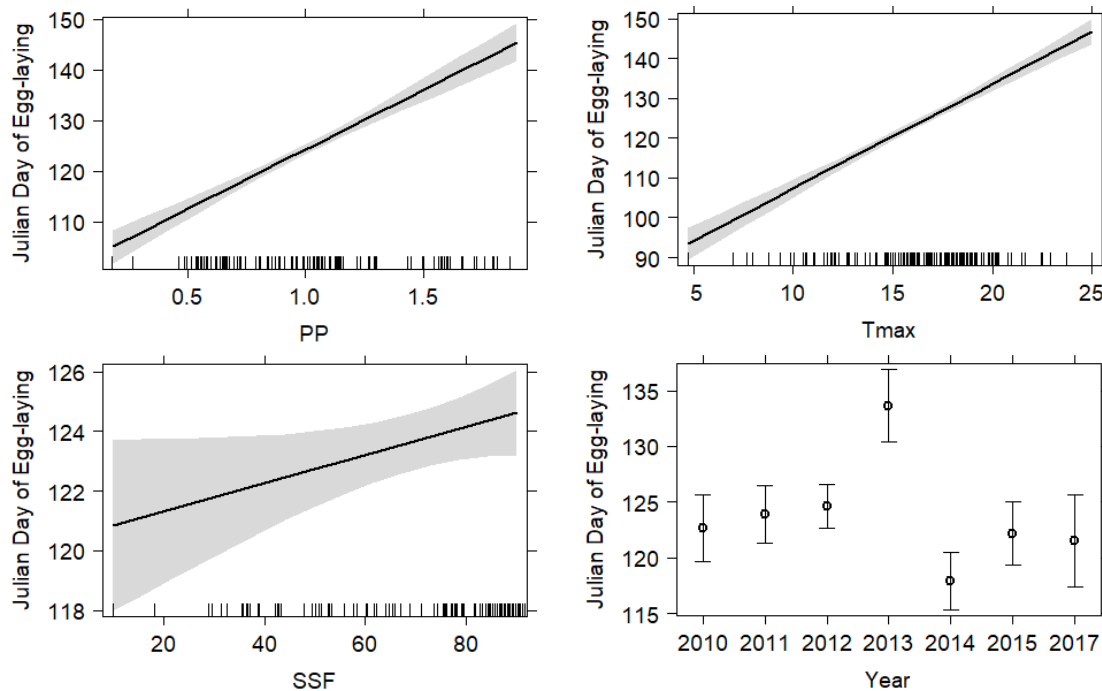

Fig. 8: The LMM on egg-laying dates featured two weather variables (PP, T_{max}), year, SSF and observer category (not depicted) as significant explanatory terms. The overall R^2LMMc was 0.77. Model details in Table 2.
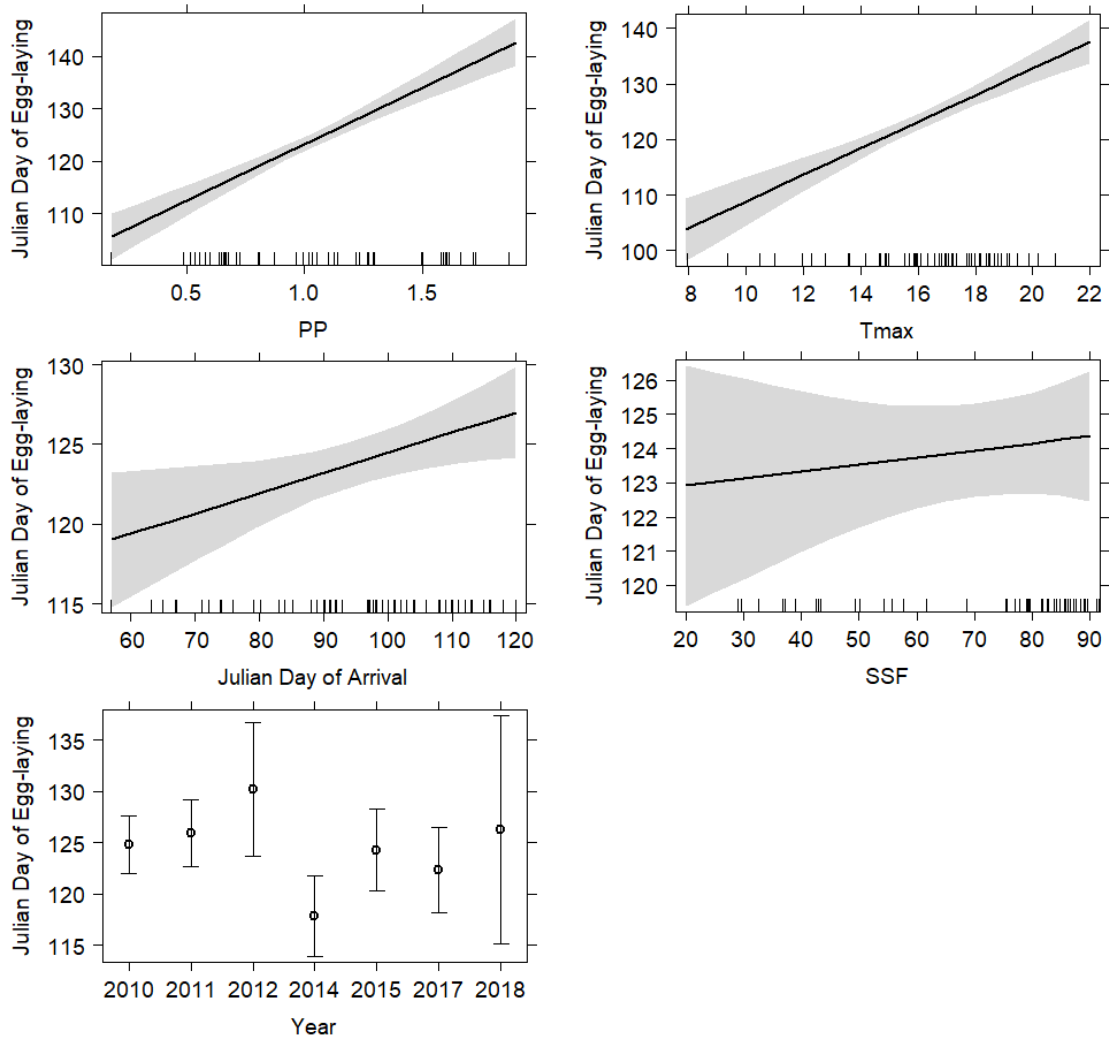
Fig. 9: The LMM on egg-laying dates from corresponding observations featured two weather variables (PP, T_{max}), year and arrival date as significant explanatory terms. SSF was not significant. The overall R^2c of the LMM was 0.85. Model details in Table 3.

Tab. 3: LMM on egg-laying dates from corresponding observations (2010-2012, 2014-2015, 2017-2018) exploring the effects of arrival date, precipitation (PP, mean from 21-79 days before egg-laying), maximum temperature (Tmax, mean from 20-40 days before egg-laying), Soil Seal Factor (SSF) and year.

	Estimate	SE	χ^2	P	Sign.	R^2LMMc
Egg-laying date ~ Arrival date + PP + T_{max} + SSF + Year + (1 | nest ID)						0.85
Arrival date	0.13	0.05	6.16	0.013	*	
PP	21.48	2.40	79.78	< 0.001	***	
T_{max}	2.39	0.32	56.78	< 0.001	***	
SSF	0.02	0.03	0.41	0.523	-	
Year†			18.34	0.005	**	
2011	1.16	2.33				
2012	5.37	3.52				
2014	-6.91	2.50				
2015	-0.52	2.41				
2017	-2.47	2.34				
2018	1.44	5.73				
Intercept	50.06	5.59	80.35	< 0.001	***	

† Year 2010 was used as a reference category; significance categories were set as '***' = P < 0.001; '**' = P < 0.01; '*' = P < 0.05.

Discussion

Our results suggest that the breeding phenology of the urban kestrels of Vienna is highly affected by weather variables. Especially precipitation proved to be the most informative variable for predicting egg-laying dates, within a time window starting before the arrival at the nest site and ending three weeks before egg-laying. Additionally, the model on egg-laying dates identified degree of urbanisation and observer category as significant factors, whilst revealing strong inter-annual variation.

Climatic variables affect egg-laying date

In general, the reproduction of birds is influenced by precipitation and temperature (Crick & Sparks, 1999), but only a more detailed identification of critical time windows allow to predict potential impacts of climate change (van de Pol & Cockburn, 2011). Our associative approach on the critical time windows (Brommer et al., 2008) revealed that the most informative time windows spanned from roughly eleven to three weeks before egg-laying for precipitation and five to three and a half weeks for temperature. The mechanistic pathways behind the influence of precipitation and temperature on egg-laying include direct effects on energetic demands of females and gonadal growth of both sexes, and indirect effects on the food source (Dunn, 2004) that in turn control prey availability and ultimately hunting success. However, a previous study on the kestrel population of Vienna verified a stronger connection between breeding performance and weather parameters than between breeding performance and diet composition (Kreiderits et al., 2016). Prey availability as such was not assessed in this study.

Our findings emphasise the role of precipitation as cue for clutch initiation, but surprisingly, the critical time windows started way before the peak of arrivals at the nest site (after migration) four to three weeks before egg-laying (Supplement, Fig. VI). We consider two potential reasons. Firstly, kestrels are short-distance migrants (Village, 1990), although the detailed wintering grounds and migration route of the Viennese kestrel population remain unknown. It is therefore possible that they might experience the same macroclimate at their wintering grounds and breeding site. In Europe, precipitation and temperature are closely related to the North Atlantic Oscillation (NAO) in terms of long-term trend and in the frequency of extreme weather events (Hurrell, 1995; Scaife et al., 2008). Both local weather and winter North Atlantic Oscillation can explain variation in egg-laying dates of Mediterranean kestrels (Costantini et al., 2010a). However, in contrast to our population the one in Rome only shows facultative winter dispersion (Costantini et al., 2010a), a phenomenon that also seems to increase in frequency in Vienna [per obs] but comprehensive data on this issue are currently missing. Secondly, previous findings

have shown that dry and mild winters have positive effects on the proportion of mammals in the kestrel's diet – which is their main prey (Kreiderits et al., 2016). In consequence, the weather before breeding might have direct and indirect effects on phenology.

Interestingly, the weather closer to the egg-laying appeared to be less influential, as the critical time windows ended three weeks before egg-laying, indicating a time gap between cue and response. The time window did not overlap with the actual development of the eggs within the body, which supposedly starts nine days before laying of the first egg (Meijer et al., 1989). Lag times are generally considered disadvantageous, as they enhance the probability of mismatches between environmental optimum and breeding effort, but time scales are dependent on the environmental variability (Padilla & Adolph, 1996).

Although both climatic variables appeared to be significant parameters in our final models, we postulate precipitation to be more informative than maximum daily temperature. Despite the inter-annual variation of weather variables and egg-laying dates it is inevitable that daily maximum temperatures will rise with increasing day of the year (Supplement, Fig. VII). Hence, we argue that earlier breeders will naturally face colder temperatures within the given time window rather than higher temperatures postponing egg-laying as implied by our models. It was hardly possible to disentangle temperature from the course of the year itself. Precipitation on the other hand showed less seasonal trends (Supplement, Fig. VIII). Higher amounts of rainfall during the critical time window delayed egg-laying, which supports previous studies (Carrillo & González-Dávila, 2009; Costantini et al., 2010a; Kreiderits et al., 2016).

Compensation of later arrival by shortening of courtship period

Another significant predictor for egg-laying date was the arrival date itself, but kestrels which arrive later at the nest site do not necessarily delay their egg-laying. The courtship period, defined as the time from arrival until egg-laying, decreased dramatically with later arrival (half a day decrease per later day of arrival). This might be a strategy to mitigate expected fitness costs of the late arrival for the offspring (Daan et al., 1989), while reducing fitness costs for the parents. Meaning, the utilisation of urban core areas as breeding territories might be linked to an attractive high nest-site availability but also a low food availability (Sumasgutner, Nemeth, et al., 2014). Because of this challenge the parents might benefit from extending their stay in probably more natural wintering habitat to gain a better body condition, which in turn heavily influences breeding productivity (Drent & Daan, 1980). Indeed, supplemented food (Dijkstra et al., 1982; Korpimäki & Wiehn, 1998) and superior hunting skills of the male (Masman et al., 1986) are known to lead to

considerably earlier laying dates in kestrels. However, in several raptor species including kestrels egg-laying date is also affected by individual age and breeding experience (Daunt et al., 1999, Sumasgutner et al., 2019; Forslund & Pärt, 1995; Sumasgutner, Vasko, et al., 2014), but also intraspecific competition for territories (e.g. Sergio et al., 2007) or social cues by conspecifics (Danchin et al., 2004; Sumasgutner, Vasko, et al., 2014) might play an important role. Ultimately, it remains difficult to assess the effect of shortened courtship periods after later arrival in an overall lower quality breeding habitat without including information on body condition, individual age and breeding experience, migration distances and quality of the wintering habitats of the observed individuals.

Observer category matters

The underlying monitoring program is designed as a citizen science project, so the data is provided by academic and citizen scientists contributing their observations. We found a significant relationship between arrival and egg-laying dates and observer category. Citizen scientists observed the arrivals of kestrels on average one week earlier than academic scientists, which is supported by our model on arrival date. This is very logical for methodological reasons. Firstly, the number of daily on-site presence of citizen scientists monitoring a nest site close to their working place or residential home is higher than of academic scientists conducting systematic monitoring of several nest sites in a short period of time. Thus, the detection probability by citizen scientists is increased. Secondly, private flats and bureaus regularly offer a direct view on nest sites and might increase the detection probability of arriving kestrels when compared to working from street level. Thirdly, the systematic monitoring by academic scientists was mobilised when the first reports of citizen scientists accumulated, so the onset of the systematic monitoring itself is induced by the activity of citizen scientists.

The difference was less pronounced for egg-laying. Nevertheless, observer category was identified as a significant factor in egg-laying dates, with citizen scientists reporting the egg-laying earlier, but very low in numbers. Compared to arrivals, which are accompanied by prominent courtship behaviour, egg-laying happens rather secretively. It is mainly noticed by observers who have a close direct view into the nest cup itself, for example in cases of broods in flowering boxes on the windowsill. The academic scientists on the other hand estimated detailed egg-laying dates mostly by back-dating during measuring, weighing and banding the nestlings(Kostrzewa & Kostrzewa, 1993; Village, 1990). Hence, we see a strong methodological constraint to this result.

We conclude that citizen scientists add valuable data to this project. Citizen science is known to decidedly increase the scale of ecological field surveys by broadening the

sample size and geographical extent and is highly valued as complementary approach in synergy with research by academic scientists (Chandler et al., 2017; Dickinson et al., 2010; Miller-Rushing et al., 2012). However, due to the above-mentioned factors, observer category should be considered when analysing data on arrival or egg-laying dates to control for variation linked to the methodology and not biotic factors.

No effect of urbanisation on arrival dates but on egg-laying dates

Interestingly, with this larger data set, we could not confirm a previous finding of earlier arrival dates in more urbanised areas (effect of the Soil Seal Factor (SSF)), even though the direction remained the same. However, die original study was limited to the years 2010-2012 and the result was only marginally significant back then (Sumasgutner, Nemeth, et al., 2014). Urbanisation indeed had a significant effect on egg-laying dates, in a way that later egg-laying was observed in more urbanised areas although confidence intervals remained large. This is remarkable, as urbanisation usually correlates positively with earlier egg-laying dates in several passerine bird species (Chamberlain et al., 2009; Jong et al., 2018; Møller et al., 2015). This shift in the breeding phenology of urban birds appears less consistently in urban raptors (Kettel et al., 2018). Furthermore, both raptors and cavity-nesting species respond less consistently to urbanisation (Marzluff, 2001). Urban breeding kestrels in Israel laid their eggs on average earlier than their conspecifics breeding in villages or towns, but these results were not significant (nevertheless, indicating a potential underlying urbanisation gradient; Charter et al., 2007). Previous studies in Vienna, including a subset of the present data, revealed no effect of SSF on egg-laying dates (Sumasgutner, Nemeth, et al., 2014).

Inter-annual variation remains

The year of observation was highly significant in all models. Concerning the annual variation of arrival dates, we suggest three main, non-exclusive reasons for temporal variation in arrival after migration: firstly, the time of departure from wintering sites could vary, secondly, migration speed could vary, and thirdly, wintering could take place in varying places, with some being closer to the breeding area (Lehikoinen et al., 2004). Ultimately, the variation explained by our model on arrival dates remains rather low, implying that we missed some important factors. In contrast, both models on egg-laying dates explain a high amount of variation.

Conclusion and further directions

It is inevitable to acquire knowledge on the wintering grounds of this population to gain deeper understanding of arrival dates and which factors might ultimately shape phenology in the species. Unfortunately, migration distances are yet unknown and so are the local weather conditions or prey availability on the wintering grounds.

However, we gained much better understanding on variation in egg-laying dates. As for arrival dates, we found a strong inter-annual variation and a significant effect of observer category. Weather variables before the on-set of breeding are well-known indicators, probably acting as cues used by the birds to predict optimal environmental conditions for breeding (Visser et al., 2012). Yet, most evidence focuses on weather conditions close to the egg-laying date itself or uses monthly means (Costantini et al., 2010a), which might limit the explained variation compared to sliding window approach (Brommer et al., 2008; Williams et al., 2015). We found that, beside precipitation and temperature, the degree of urbanisation was another important factor, with kestrels breading in less urban areas laying their clutches earlier than their conspecifics in urban core areas.

When testing the effect of arrival date on egg-laying dates for all cases in which both dates were recorded within the same year, we found a shortened courtship period in later arriving breeding pairs, resulting in relatively earlier egg-laying. Later clutches generally face higher fitness costs and are less likely to produce offspring which recruits into the breeding population (Perrins, 1970). The shortening of the courtship period might be a strategy to mitigate the negative effects of later broods while taking advantage of potentially favourable condition at the wintering ground. Ultimately, this would add to the body of evidence that kestrels behaviourally adapt to urban environments, despite our concern about cities posing an ecological trap on them (Sumasgutner, Nemeth, et al., 2014). Considering their potential ability to use environmental cues for the fine-tuning of breeding phenology to the environmental optimum, European kestrels might be able to adapt to the human-induced climate change.

Zusammenfassung

Das Eiablagedatum (sub)urban brütender Turmfalken *Falco tinnunculus* in Wien ist stark beeinflusst durch die Niederschlagsmenge innerhalb eines kritischen Zeitraums vor der Rückkehr aus den Überwinterungsgebieten bis drei Wochen vor der Eiablage. Der große Einfluss von Umweltvariablen wie Niederschlag und Temperatur als flexible Zeitgeber zur Festlegung eines idealen Brut- und Eiablagezeitpunktes ist für viele Vogelarten schon lange bekannt. Gerade diese Abhängigkeit bringt jedoch durch den vom Menschen verursachten Klimawandel große Risiken mit sich, wodurch sich zunehmend die Frage nach dem genauen zeitlichen und funktionalen ökologischen Zusammenhang stellt. Ziel unserer Studie war deshalb die Untersuchung der großen Variation von Rückkehr- und Eiablagezeitpunkt der Turmfalkenpopulation in Wien (415 km^2), Österreich. Wir analysierten die von 2010-2018 gemeinsam von Citizen Scientists und professionellen Wissenschaftlern/innen erhobenen Ankunfts- und Eiablagebeobachtungen. Neben dem Urbanisierungsgrad, der Beobachtergruppe und dem Beobachtungsjahr verwendeten wir einen «sliding window approach» zur Identifikation kritischer Zeitfenster, welche in direktem Zusammenhang mit dem Eiablagedatum stehen. Weiters untersuchten wir den Zusammenhang zwischen der Rückkehr ins Brutgebiet und der Dauer bis zur Eiablage. Unsere Ergebnisse zeigten eine Abhängigkeit des festgestellten Zeitpunkts der Rückkehr ins Brutgebiet von der Beobachtergruppe und dem Beobachtungsjahr, während der Urbanisierungsgrad hingegen keine Rolle spielen dürfte. Alle berücksichtigten Variablen zeigten jedoch einen signifikanten Einfluss auf das Eiablagedatum. Citizen Scientists stellten Rückkehr- und Eiablagezeitpunkt früher als Wissenschaftler/innen fest. Später rückkehrende Turmfalken zeigten deutlich kürzere Zeitfenster zwischen Rückker und Eiablage. Urbanisierung, Beobachterkategorie und die zuvor gefallene Niederschlagsmenge erwiesen sich somit als wichtige Faktoren mit großem Einfluss auf das Eiablagedatum. Auch Temperatur zeigte einen signifikanten Einfluss auf die Eiablage, korrelierte aber zu stark mit dem Jahresverlauf, um ihre tatsächliche Bedeutung aufzeigen zu lassen. Eine verzögerte Ankunft im Brutgebiet kann durch eine relativ frühere Eiablage kompensiert werden. Diese Verhaltensanpassung könnte erlauben, die Nachteile der Brutvorbereitung in einem suboptimalen Bruthabitat auf ein kürzeres Zeitfenster zu reduzieren, ohne eine Reduktion des Bruterfolges zu riskieren.

References

Adrion, M. (2016). *Carotenoid colouration and health status of urban Kestrels (*Falco tinnunculus*)*. University of Vienna.

Antrop, M. (2004). Landscape change and the urbanization process in Europe. *Landscape and Urban Planning*, *67*(1–4), 9–26.

Arnfield, A. J. (2003). Two decades of urban climate research: A review of turbulence, exchanges of energy and water, and the urban heat island. *International Journal of Climatology*, *23*(1), 1–26.

Baker, J. R. (1938). The evolution of breeding seasons. In G. R. Beer (Ed.), *Evolution: essays on aspects of evolutionary biology* (pp. 161–177). Oxford University Press.

Barton, K. (2019). *Multi-Model Inference* (1.43.6). https://cran.r-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology*, *18*(6), 1482–1491.

Beichle, U. (1980). Siedlungsdichte, Jagdreviere und Jagdweise des Turmfalken (*Falco tinnunculus*) im Stadtgebiet von Kiel. *Corax*, *8*, 3–12.

Blair, R. B. (1996). Land Use and Avian Species Diversity Along an Urban Gradient. *Ecological Applications*, *6*(2), 506–519.

Bonney, R., Cooper, C. B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V., & Shirk, J. (2009). Citizen Science: A Developing Tool for Expanding Science Knowledge and Scientific Literacy. *BioScience*, *59*(11), 977–984.

Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, *78*(1), 73–83.

Brommer, J. E., Rattiste, K., & Wilson, A. J. (2008). Exploring plasticity in the wild: Laying date-temperature reaction norms in the common gull *Larus canus*. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 687–693.

Burgess, H. K., DeBey, L. B., Froehlich, H. E., Schmidt, N., Theobald, E. J., Ettinger, A. K., HilleRisLambers, J., Tewksbury, J., & Parrish, J. K. (2017). The science of citizen science: Exploring barriers to use as a primary research tool. *Biological Conservation*, *208*, 113–120.

Carrillo, J., & González-Dávila, E. (2009). Latitudinal variation in breeding parameters of the common kestrel *Falco tinnunculus*. *Ardeola*, *56*(2), 215–228.

Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., & Gaston, K. J. (2009). Avian productivity in urban landscapes: A review and meta-analysis. *Ibis*, *151*(1), 1–18.

Chandler, M., See, L., Copas, K., Bonde, A. M. Z., López, B. C., Danielsen, F., Legind, J. K., Masinde, S., Miller-Rushing, A. J., Newman, G., Rosemartin, A., & Turak, E. (2017). Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, *213*, 280–294.

Charter, M., Izhaki, I., Bouskila, A., & Leshem, Y. (2007). Breeding Success of the Eurasian Kestrel (*Falco tinnunculus*) Nesting on Buildings in Israel. *Journal of Raptor Research*, *41*(2), 139–143.

Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Body condition and seabird reproductive performance: a study of three petrel species. *Ecology*, *76*(7), 2240–2246.

Cooper, C. B., Shirk, J., & Zuckerberg, B. (2014). The invisible prevalence of citizen science in global research: Migratory birds and climate change. *PLoS ONE*, *9*(9).

Costantini, D., Carello, L., & Dell'Omo, G. (2010a). Patterns of covariation among weather conditions, winter North Atlantic Oscillation index and reproductive traits in Mediterranean kestrels. *Journal of Zoology*, *280*(2), 177–184.

Costantini, D., Carello, L., & Dell'Omo, G. (2010b). Temporal covariation of egg volume and breeding conditions in the Common Kestrel (*Falco tinnunculus*) in the Mediterranean region. *Ornis Fennica*, *87*(4), 144–152.

Crick, H. Q. P., & Sparks, T. H. (1999). Climate change related to egg-laying trends. *Nature*, *399*, 423–424.

Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic Associations among Causes of Species Endangerment in the United States. *BioScience*, *50*(7), 593–601.

Daan, S., Dijkstra, C., Drent, R., & Meijer, T. (1989). Food supply and the annual timing of avian reproduction. In H. Ouellet (Ed.), *Acta XIX Congressus Internationalis Ornithologici, Volume I: Proceedings XIX International Ornithological Congress, 1986, Ottawa* (Vol. 1, pp. 392–407). University of Ottawa Press.

Daan, S., & Tinbergen, J. M. (1997). Adaptation of Life Histories. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach* (4th Editio, pp. 311–333). Oxford University Press.

Danchin, É., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, *305*(5683), 487–491.

Daunt, F., Wanless, S., Harris, M. P., & Monaghan, P. (1999). Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1427), 1489–1493.

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*, *41*, 149–172.

Dijkstra, C., Vuursteen, L., Daan, S., & Masman, D. (1982). Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis*, *124*(2), 210–213.

Drent, R. H., & Daan, S. (1980). The Prudent Parent: Energetic Adjustments in Avian Breeding 1). *Ardea*, *38–90*, 225–252.

Dunn, P. (2004). Breeding dates and reproductive performance. *Advances in Ecological Research*, *35*, 69–87.

Dwernychuk, L. W., & Boag, D. A. (1972). Ducks nesting in association with gulls—An ecological trap? *Canadian Journal of Zoology*, *50*(5), 559–563.

Dykstra, C. R., Bloom, P. H., & McCrary, M. D. (2018). Red-Shouldered Hawks: Adaptable Denizens of the Suburbs. In *Urban Raptors* (pp. 110–125). Springer.

Dykstra, C. R., Hays, J. L., Daniel, F. B., & Simon, M. M. (2001). Home range and habitat use of suburban Red-shouldered Hawks in southwestern Ohio. *The Wilson Journal of Ornithology*, *113*(3), 308–317.

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*(7002), 881–884.

ESRI Inc. (2017). *ArcGIS Desktop 10.6*.

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends in Ecology & Evolution*, *10*(9), 374–378.

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd edition). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Fretwell, S. D. (1972). *Populations in a seasonal environment* (Vol. 5). Princeton University Press.

Gamauf, A. (1991). *Greifvögel in Österreich. Bestand, Bedrohung, Gesetz [Birds of Prey in Austria. Population – Threat – Law]*. Umweltbundesamt.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, *319*(5864), 756–760.

Grüebler, M. U., & Naef-Daenzer, B. (2010). Fitness consequences of timing of breeding in birds: Date effects in the course of a reproductive episode. *Journal of Avian Biology*, *41*(3), 282–291.

Harriman, V. B., Dawson, R. D., Bortolotti, L. E., & Clark, R. G. (2017). Seasonal patterns in reproductive success of temperate-breeding birds: Experimental tests of the date and quality hypotheses. *Ecology and Evolution*, *7*(7), 2122–2132.

Hendry, A. P., Gotanda, K. M., & Svensson, E. I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712).

Holte, D., Köppen, U., & Schmitz-Ornés, A. (2016). Partial Migration in a Central European Raptor Species: An Analysis of Ring Re-Encounter Data of Common Kestrels *Falco tinnunculus*. *Acta Ornithologica*, *51*(1), 39–54.

Huhta, E., & Jokimäki, J. (2008). Breeding occupancy and success of two hole-nesting passerines: the impact of fragmentation caused by forestry. *Ecography*, *24*(4), 431–440.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic oscillation: Regional temperatures and precipitation. *Science*, *269*(5224), 676–679.

Inouye, D. W. (2008). Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. *Ecology*, *89*(2), 353–362.

Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*(6), 1211–1219.

Jong, M. de, Eertwegh, L. van den, Beskers, R. E., Vries, P. P. de, Spoelstra, K., & Visser, M. E. (2018). Timing of Avian Breeding in an Urbanised World. *Ardea*, *106*(1), 31.

Kassambara, A. ((2019). *"ggplot2" Based Publication Ready Plots*. https://rpkgs.datanovia.com/ggpubr/

Kettel, E. F., Gentle, L. K., Quinn, J. L., & Yarnell, R. W. (2018). The breeding performance of raptors in urban landscapes: a review and meta-analysis. *Journal of Ornithology*, *159*(1), 1–18.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*, 940–950.

Kokko, H., & Sutherland, W. J. (2001). Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research*, *3*(5), 537–551.

Korpimäki, E. (1986). Diet variation, hunting habitat and reproductive output of the kestrel *Falco tinnunculus* in the light of the optimal diet theory. *Ornis Fennica*, *63*, 84–90.

Korpimäki, E., & Wiehn, J. (1998). Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos*, 259–272.

Kostrzewa, R., & Kostrzewa, A. (1993). *Der Turmfalke: Überlebensstrategien eines Greifvogels [The Kestrel: Survival strategies of a raptor species]*. Aula-Verlag.

Kreiderits, A., Gamauf, A., Krenn, H. W., & Sumasgutner, P. (2016). Investigating the influence of local weather conditions and alternative prey composition on the breeding performance of urban Eurasian Kestrels *Falco tinnunculus*. *Bird Study*, *63*(3), 369–379.

Kristan, W. B. (2003). The role of habitat selection behavior in population dynamics: Source-sink systems and ecological traps. *Oikos*, *103*(3), 457–468.

Kübler, S., Kupko, S., & Zeller, U. (2005). The kestrel (*Falco tinnunculus* L.) in Berlin: Investigation of breeding biology and feeding ecology. *Journal of Ornithology*, *146*(3), 271–278.

Lancaster, R. K., & Rees, W. E. (1979). Bird communities and the structure of urban habitats. *Canadian Journal of Zoology*, *57*(12), 2358–2368.

Lehikoinen, E., Sparks, T. H., & Zalakevicius, M. (2004). Arrival and Departure Dates. *Advances in Ecological Research*, *35*, 1–31.

Lieth, H. (1970). Phenology in productivity studies. In D. Reichle (Ed.), *Analysis of Temperate Forest Ecosystems* (p. 29). Springer Berlin Heidelberg.

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian Ecology and Conservation in an Urbanizing World* (pp. 19–47). Springer.

Masman, D., Gordijn, M., Daan, S., & Dijkstra, C. O. R. (1986). Ecological energetics of the kestrel: field estimates of energy intake throughout the year. *Ardea*, *74*, 24–39.

McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, *52*(10), 883–890.

Meijer, T., Deerenberg, C., Daan, S., & Dijkstra, C. (1992). Egg-Laying and Photorefractoriness in the European Kestrel *Falco tinnunculus*. *Ornis Scandinavica*, *23*(3), 405–410.

Meijer, T., Masman, D., & Daan, S. (1989). Energetics of Reproduction in Female Kestrels. *The Auk*, *106*(4), 549–559.

Mikula, P., Hromada, M., & Tryjanowski, P. (2013). Bats and swifts as food of the European kestrel (*Falco tinnunculus*) in a small town in Slovakia. *Ornis Fennica*, *90*(3), 178–185.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3177–3186.

Miller-Rushing, A. J., Primack, R., & Bonney, R. (2012). The history of public participation in ecological research. *Frontiers in Ecology and the Environment*, *10*(6), 285–290.

Møller, A. P., Díaz, M., Grim, T., Dvorská, A., Flensted-Jensen, E., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Markó, G., Szymański, P., & Tryjanowski, P. (2015). Effects of urbanization on bird phenology: A continental study of paired urban and rural populations. *Climate Research*, *66*(3), 185–199.

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(42), 16195–16200.

Municipal Department 23 - Economy, L. and S. (2018). *Statistisches Jahrbuch der Stadt Wien [Yearbooks of the City of Vienna]*. City of Vienna.

Murton, R. K., & Westwood, N. J. (1977). *Avian Breeding Cycles*. Clarenden Press.

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*(134).

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50.

Oke, T. R. (1982). The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society*, *108*, 1–24.

Padilla, D. K., & Adolph, S. C. (1996). Plastic inducible morphologies are not always adaptive: The importance of time delays in a stochastic environment. *Evolutionary Ecology*, *10*(1), 105–117.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42.

Perrins, C. M. (1970). The Timing of Birds' Breeding Seasons. *Ibis*, *112*(2), 242–255.

Pimm, S. L., & Raven, P. (2000). Extinction by numbers. *Nature*, *403*(6772), 843–845.

R Core Team. (2019). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.r-project.org/

Renner, S. S., & Zohner, C. M. (2018). Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 165–182.

Riegert, J., Dufek, A., Fainová, D., Mikeš, V., & Fuchs, R. (2007). Increased hunting effort buffers against vole scarcity in an urban Kestrel *Falco tinnunculus* population. *Bird Study*, *54*(3), 353–361.

Riegert, J., Fainová, D., Mikeš, V., & Fuchs, R. (2007). How urban Kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation? *Acta Ornithologica*, *42*(1), 69–76.

Riegert, J., & Fuchs, R. (2011). Fidelity to roost sites and diet composition of wintering male urban Common Kestrels *Falco tinnunculus*. *Acta Ornithologica*, *46*(2), 183–189.

Roberts, L. (2011). 9 Billion? *Science*, *333*(6042), 540–544.

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, *87*(5), 1075–1085.

Romanowski, J. (1996). On the diet of urban kestrel (*Falco tinnunculus*) in Warsaw. *Buteo*, *8*, 123–130.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918), 57–60.

Rutz, C. (2006). Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *ARDEA-WAGENINGEN-*, *94*(2), 185.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L. R., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774.

Sarkar, D. (2008). *Lattice: Multivariate Data Visualization with R*. Springer. http://lmdvr.r-forge.r-project.org

Scaife, A. A., Folland, C. K., Alexander, L. V., Moberg, A., & Knight, J. R. (2008). European climate extremes and the North Atlantic Oscillation. *Journal of Climate*, *21*(1), 72–83.

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology and Evolution*, *17*(10), 474–480.

Secretariat of the Convention on Biological Diversity. (2006). *Global Biodiversity Outlook 2*.

Sergio, F., Blas, J., Forero, M. G., Donázar, J. A., & Hiraldo, F. (2007). Sequential settlement and site dependence in a migratory raptor. *Behavioral Ecology*, *18*(5), 811–821.

Sharp, P. J. (1996). Strategies in avian breeding cycles. *Animal Reproduction Science*, *42*(1–4), 505–513.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J., & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecology Letters*, *17*(8), 942–950.

Stenseth, N. C., & Mysterud, A. (2002). Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(21), 13379–13381.

Streutker, D. R. (2003). Satellite-measured growth of the urban heat island of Houston, Texas. *Remote Sensing of Environment*, *85*(3), 282–289.

Sumasgutner, P., Adrion, M., & Gamauf, A. (2018). Carotenoid coloration and health status of urban Eurasian kestrels (*Falco tinnunculus*). *PLoS ONE*, *13*(2), 1–21.

Sumasgutner, P., Koeslag, A., & Amar, A. (2019). Senescence in the city: exploring ageing patterns of a long-lived raptor across an urban gradient. *Journal of Avian Biology*, *50*(12), 1–14.

Sumasgutner, P., Krenn, H., Düesberg, J., Gaspar, T., & Gamauf, A. (2013). Diet specialisation and breeding success along an urban gradient: the kestrel (*Falco tinnunculus*) in Vienna, Austria. *Beiträge Zur Jagd Und Wildforschung*, *38*, 385–397.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. W., & Gamauf, A. (2014). Hard times in the city-attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology*, *11*(48).

Sumasgutner, P., Schulze, C. H., Krenn, H. W., & Gamauf, A. (2014). Conservation related conflicts in nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey. *Landscape and Urban Planning*, *127*, 94–103.

Sumasgutner, P., Vasko, V., Varjonen, R., & Korpimäki, E. (2014). Public information revealed by pellets in nest sites is more important than ecto-parasite avoidance in the settlement decisions of Eurasian kestrels. *Behavioral Ecology and Sociobiology*, *68*(12), 2023–2034.

Terraube, J., Vasko, V., & Korpimäki, E. (2015). Mechanisms and reproductive consequences of breeding dispersal in a specialist predator under temporally varying food conditions. *Oikos*, *124*(6), 762–771.

Tilman, D., & Lehman, C. (2001). Human-caused environmental change : Impacts on plant diversity and evolution Environmental Constraints in Plant Communities. *Proceedings of the National Academy of Sciences*, *98*(10), 5433–5440.

Tremblay, A., & Ransijn, J. (2015). *Model Selection and Post-hoc Analysis for (G)LMER Models* (2.10). https://cran.r-project.org/package= LMERConvenienceFunctions

United Nations. (2019). *World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420)*. United Nations.

Valkama, J., Korpimäki, E., & Tolonen, P. (1995). Habitat utilization, diet and reproductive success in the kestrel in a temporally and spatially heterogeneous environment. *Ornis Fennica*, *72*(2), 49–61.

van de Pol, M., & Cockburn, A. (2011). Identifying the critical climatic time window that affects trait expression. *American Naturalist*, *177*(5),

Verboven, N., & Visser, M. E. (1998). Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos*, 511–524.

Verhulst, S., & Nilsson, J. Å. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 399–410.

Village, A. (1990). *The Kestrel*. T & AD Poyser Ltd.

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569.

Visser, M. E., Caro, S. P., Oers, K. Van, Schaper, S. V., & Helm, B. (2010). Phenology, seasonal timing and circannual rhythms: Towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3113–3127.

Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, *147*(1), 164–172.

Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, *153*(Suppl. 1), 75–84.

Vitousek, P. M. (1994). Beyond global warming: ecology and global change. *Ecology*, *75*(7), 1861–1876.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389–395.

Wichmann, G., Dvorak, M., Teufelbauer, N., & Berg, H.-M. (2009). *Die Vogelwelt Wiens: Atlas der Brutvöge*. Verlag des Naturhistorischen Museums Wien.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer US. https://ggplot2.tidyverse.org

Williams, T. D., Bourgeon, S., Cornell, A., Ferguson, L., Fowler, M., Fronstin, R. B., & Love, O. P. (2015). Mid-winter temperatures, not spring temperatures, predict breeding phenology in the European starling *Sturnus vulgaris*. *Royal Society Open Science*, *2*(1).

Wingfield, J. C. (1983). Environmental and endocrine control of avian reproduction - an ecological approach. In S. Mikami, K. Homma, & M. Wada, (Eds.), *Avian endocrinology: environmental and ecological perspectives* (pp. 265–288). Springer.

Zohner, C. M. (2019). Phenology and the city. *Nature Ecology & Evolution*, *3*(12), 1618–1619.

Supplement

Tab. I: Land cover categories of the land allocation maps of the Environmental Protection Bureau of Vienna (MA 22 – Umwelt) and their classification in impervious and unsealed surfaces.

Class_Code	Description_German	Descretion_English	Category
11	Gebäude	Building	impervious
12	Überbauung, Verbindungsgang zwischen Häusern	Superstruction	impervious
13	Flugdach	Flying roof	impervious
14	Glashaus	Greenhouse	impervious
16	Brückenpfeiler	Pier	impervious
19	Sonstige Gebäudefläche (Nebengebäude, …)	Other Building Areas	impervious
21	Fahrbahn (Haupt-, Nebenfahrbahn, Autobahn, Radweg)	Roadway	impervious
22	Verkehrsinsel	Traffic island	impervious
23	Gehsteig, Geh-, Radweg und Stationsbereich im öffentlichen Gut	Pavement	impervious
24	Fußgängerzone	Pedestrian zone	impervious
25	Fläche für Fußgänger und Radverkehr auf Privatgrund	Pavement, bikeway on private grounds	impervious
26	Verkehrsfläche auf Privatgrund (wenn vorrangig für Autoverkehr, z.B. Einfahrten, Parkplätze, …)	Traffic area on private grounds	impervious
27	Schienenbereich	Railway area	impervious
28	Selbstständiger Gleiskörper (Straßenbahn, U-Bahn)	Autonomous railway	impervious
29	Bahnhofsbereich, Gleiskörper (ÖBB)	Railway station (OEBB)	impervious
30	Zebrastreifen	Pedestrian crossing	impervious
31	Straßenmobilar	Street furniture	impervious
32	Fahrbahnaufwölbung (Schwelle), Einfahrtsrampe	Speed ramp, road hump	impervious
33	Parkplatz im öffentlichen Gut	Public parking	impervious
39	Sonstige Verkehrsfläche	Other traffic area	impervious
41	Natürliches Gewässer, Badesee	Natural water body, bathing lake	unsealed
42	Schwimmbecken, Biotop (auf Privatgrund)	Pool, pond on private ground	unsealed
43	Brunnen (im Park), künstliche Wasserfläche (auf öffentlichen Flächen)	Fountain, artificial water body on public ground	unsealed
44	Gerinne	Gutter	unsealed
49	Sonstige Gewässerfläche	Other water surface	unsealed
51	Hof, Innenhof (bei Gebäuden)	Yard, backyard	unsealed
52	Wald, Fläche mit Baumbestand	Wood	unsealed
53	Wiese, naturnahe Grünfläche	Meadow, near-natural green land	unsealed

|			
54	Feld, Acker, Beet, Baumschule, Obstgarten, landwirtschaftlich genutzte Fläche	Aggriculturally used area	unsealed
55	Weingarten	Vineyard	unsealed
57	Gräberfeld	Graveyard	unsealed
58	Grünfläche (kultivierte Wiese, Rasen), sonstige unversiegelte Fläche	Green area (lawn), other unsealed surface	unsealed
59	Befestigte (versiegelte) Fläche auf Privatgrund (wenn nicht 25 oder oder 26)	Other impervious surface on private ground	impervious
60	Baustelle, Baugrube	Construction area	impervious
61	Sportfeld (Rasenfläche Sportplatz, Tennisplatz, Hartplatz, Eislaufplatz)	Sporting field	unsealed
62	Deponie	Landfill	impervious
63	Lagerplatz	Stockyard	impervious
64	Schottergrube	Gravel pit	unsealed
69	Sonstige Grünfläche	Other green area	unsealed
71	Mauer, Mauer im Sinne einer Einfriedung, Stützmauer	Wall, mural	impervious
73	Sockelzaun	Fence	impervious
74	Stiege, Stufe, Rollstuhl-, Kinderwagenrampe	Stairway, pedestrian ramp	impervious
81	Denkmal	Monument, memorial	impervious
82	Telefonzelle	Telephone booth	impervious
83	Stationseinrichtung (öffentlicher Verkehr)	Public transport facility	impervious
84	Kiosk, Würstelstand	Kiosk, snack stall	impervious
86	Portal	Portal	impervious
91	Rohrleitung	Pipeline	impervious
92	Energieversorgung	Energy supply	impervious
93	Klärbecken	Sewage plant (water body)	unsealed
99	Sonstige nicht zuordenbare Fläche	Other area	impervious
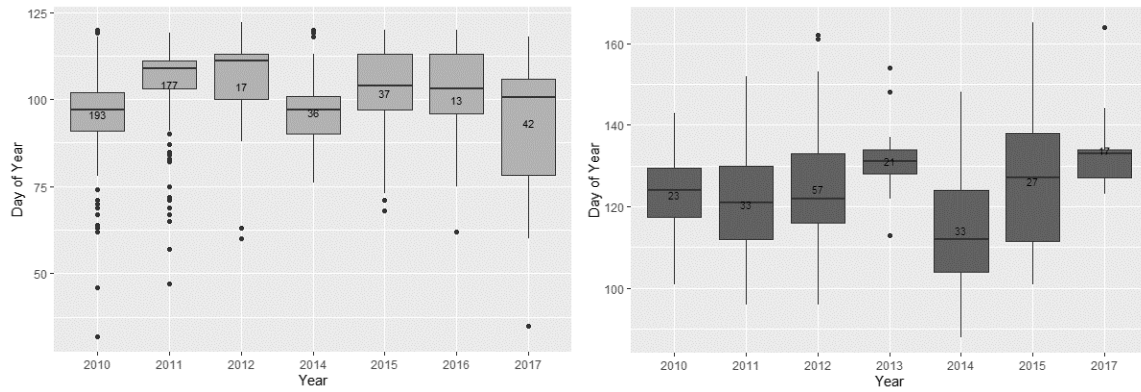
Fig. I: Distribution of total observed arrival dates (left, n = 515) and egg-laying dates (right, n = 211) pooled by year. For arrival dates, observations of the years 2013 and 2018 needed to be excluded due to less systematic monitoring and fewer data points. The same applies to the years 2016 and 2018 for egg-laying observations.
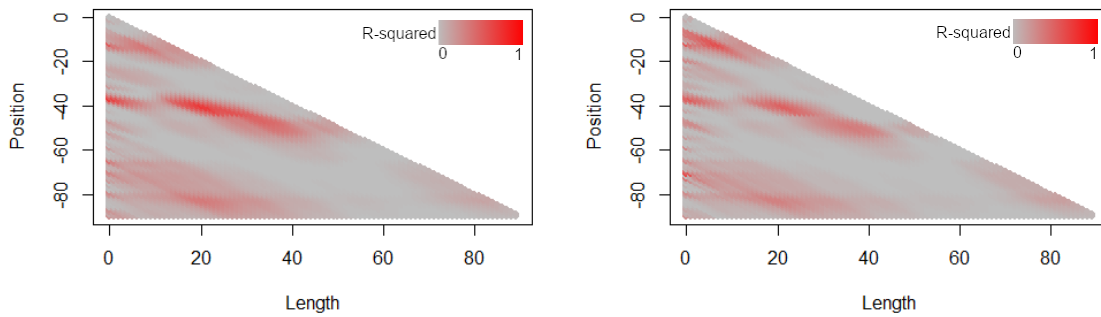

Fig. II: Depiction of R^2-values derived by the sliding window approach on average temperature (T_{ave}, left) and daily minimum temperature (T_{min}, right).
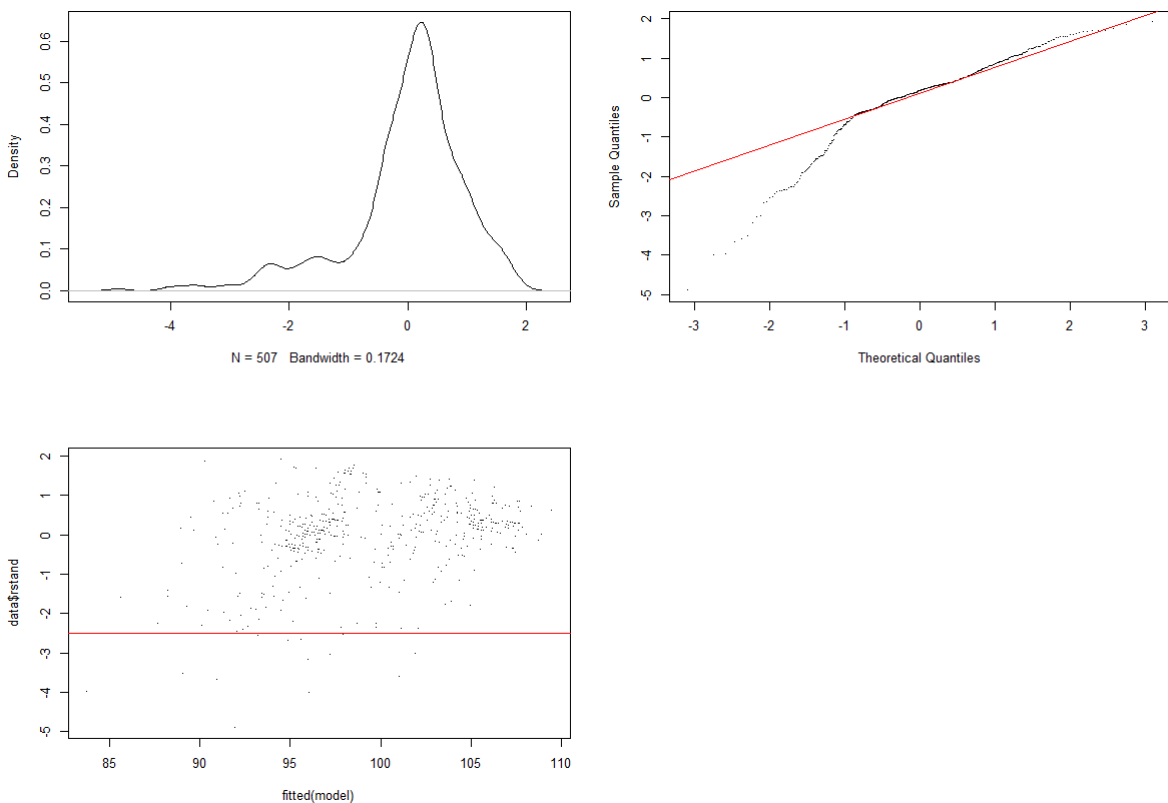

Fig. III: Model criticism plots for final model on arrival dates (n = 515).
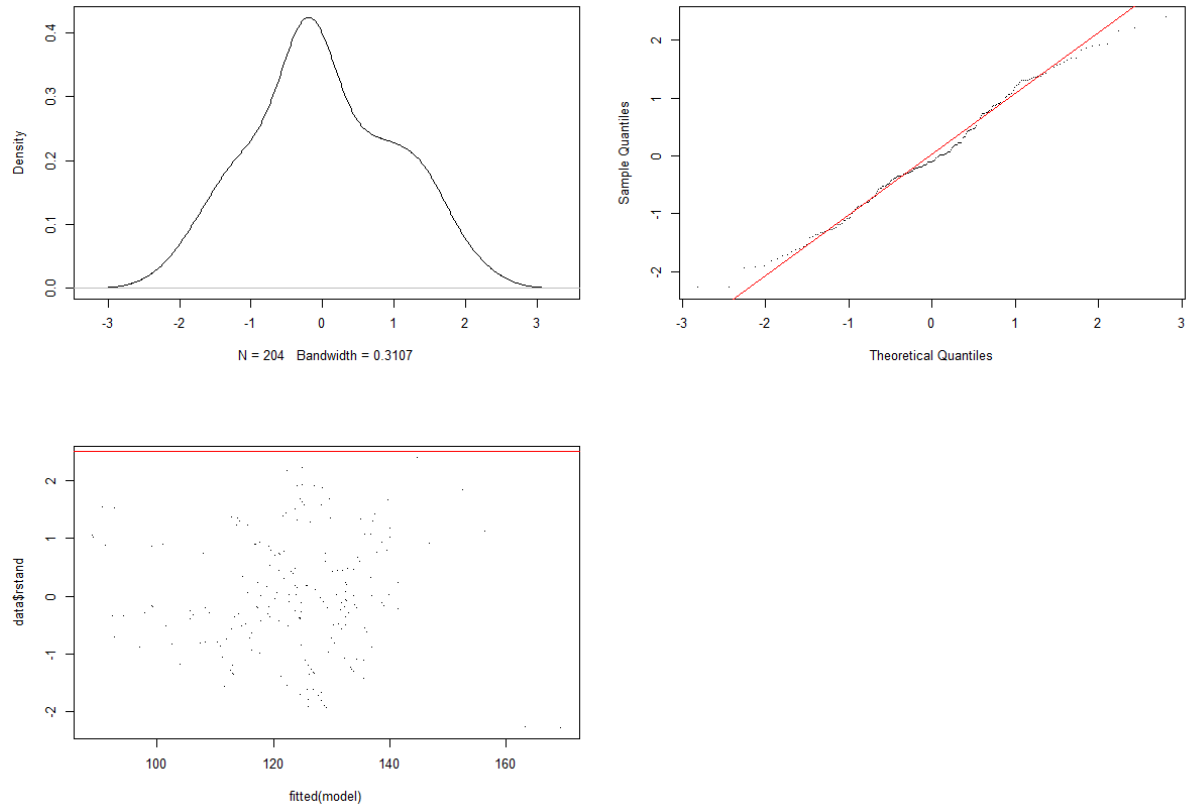
Fig. IV: Model criticism plots for final model on egg-laying dates (n = 211).
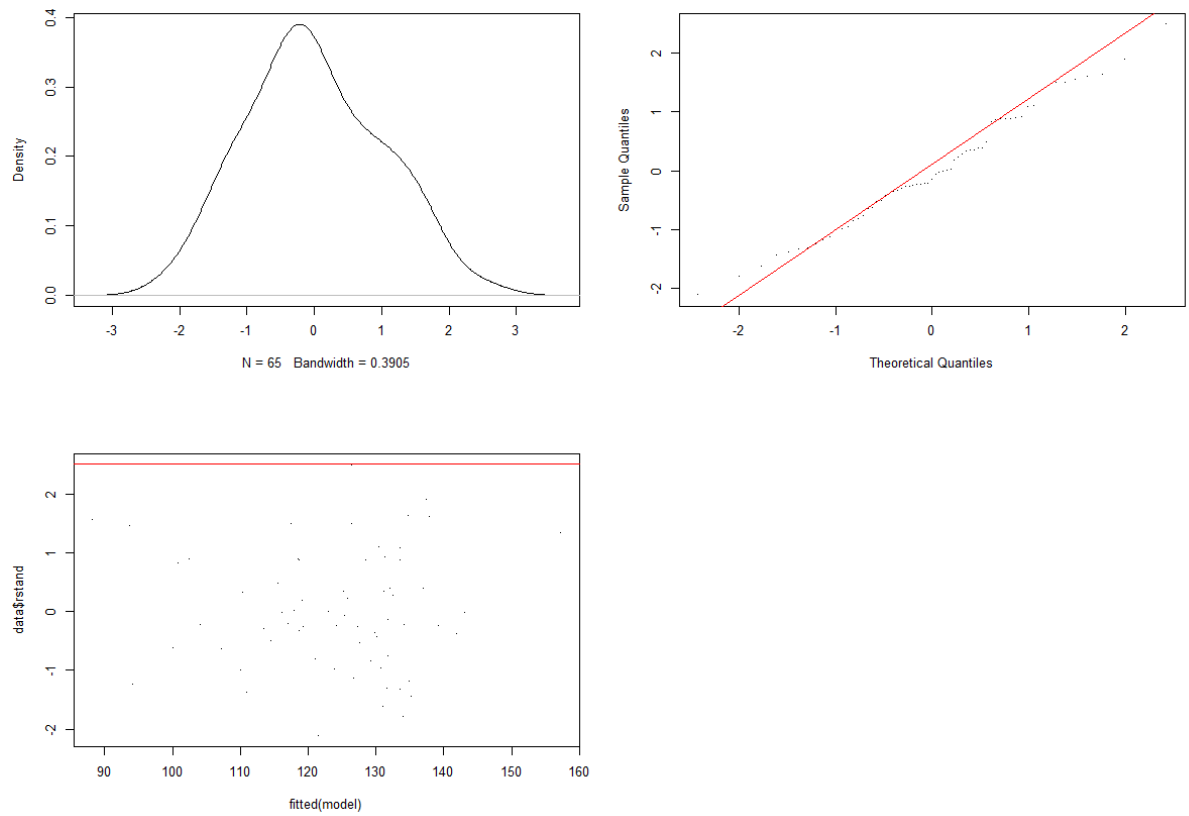

Fig. V: Model criticism plots for final model on egg-laying dates using the corresponding observations data set (n = 268).
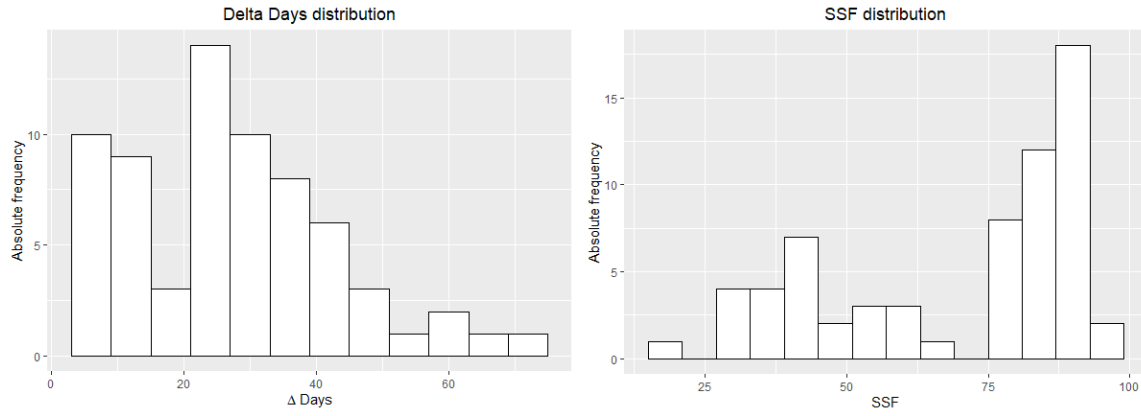
Fig. VI: Absolute frequencies of Δ Days (left) and SSF (right) of the corresponding observations data set.
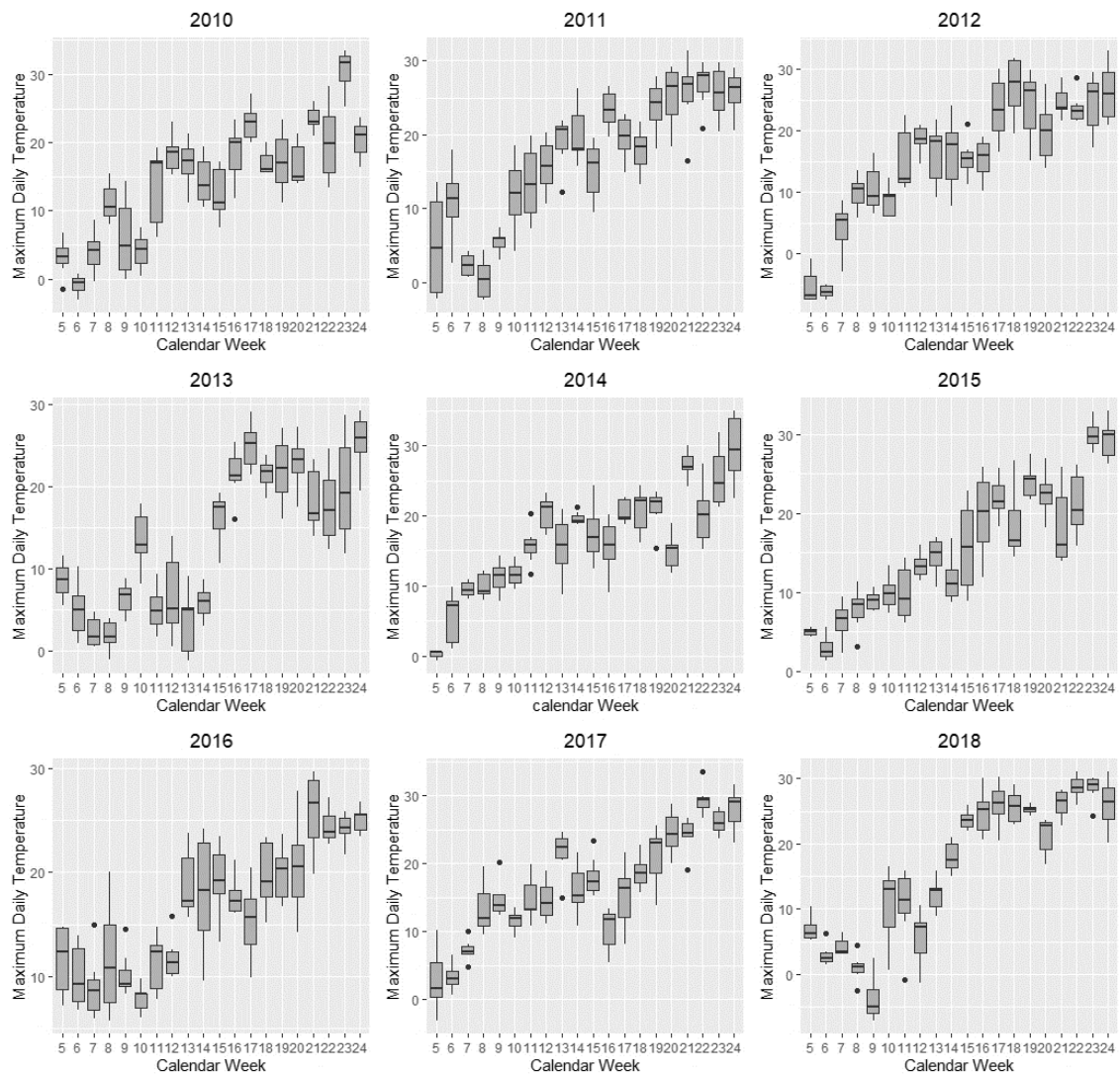

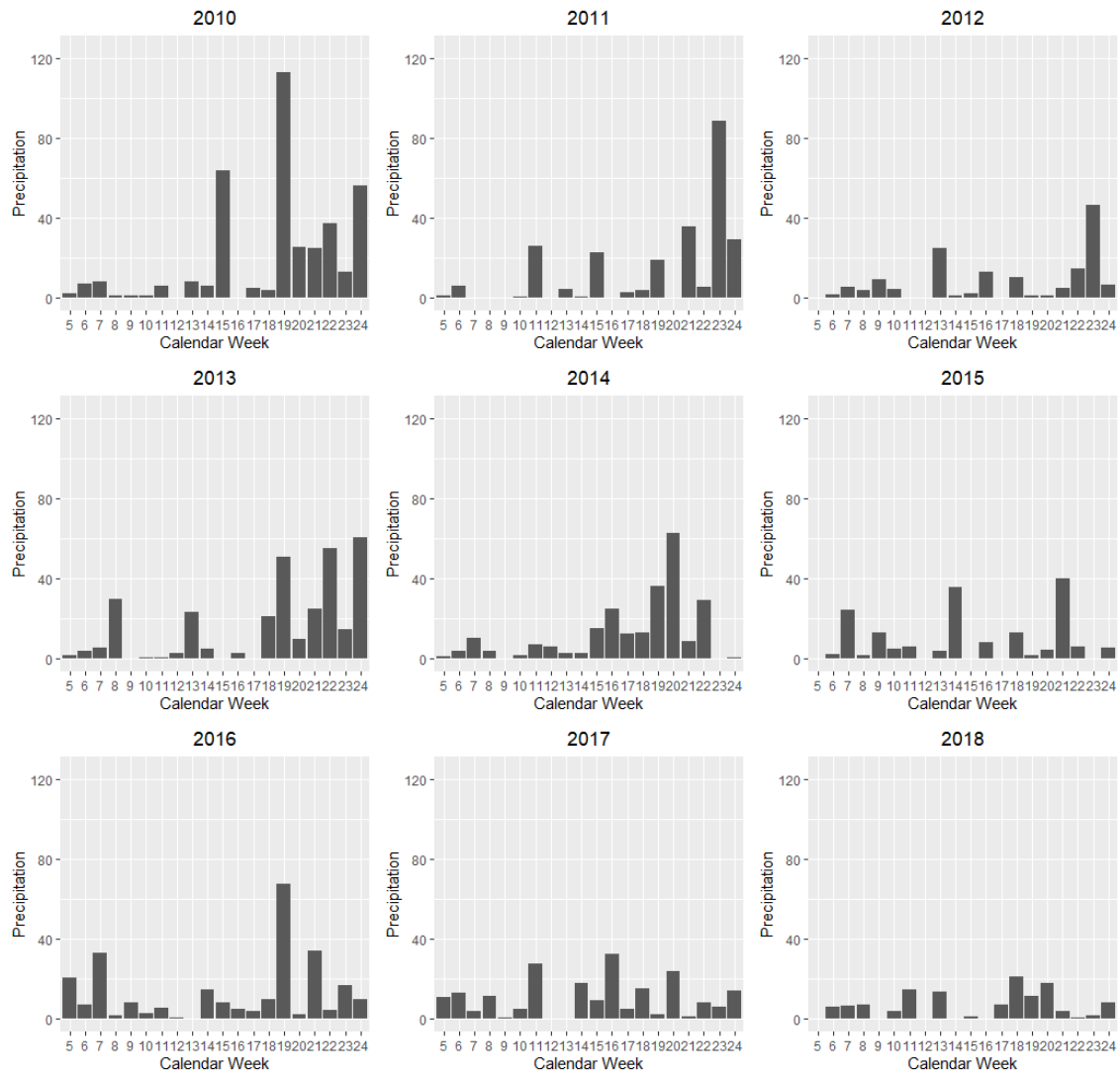Fig. VII: Daily maximum temperature [°C] per calendar week from 2010 to 2018.

Fig. VIII: Precipitation [mm] per calendar week from 2010 to 2018.