Investigating the influence of local weather conditions and alternative prey composition on the breeding performance of urban Eurasian Kestrels *Falco tinnunculus*

A. Kreiderits\(^a,b\), A. Gamauf\(^a,b\), H. W. Krenna\(^a\) and P. Sumasgutner\(^a,b,c\)

\(^a\)Department of Integrative Zoology, University of Vienna, Vienna, Austria; \(^b\)Museum of Natural History Vienna, Vienna, Austria; \(^c\)Percy FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

**ABSTRACT**

**Capsule:** Local weather conditions, but not a city-associated diet composition, influence the breeding performance of urban Eurasian Kestrels *Falco tinnunculus*.

**Aims:** We aim to explore the impact of diet composition, specifically a high proportion of avian prey, on the breeding performance of urban Eurasian Kestrels under different weather conditions.

**Methods:** The Eurasian Kestrel is known to exploit cities and occurs in the study area of Vienna, Austria (415 km\(^2\)) at high breeding densities of 89–122 pairs/100 km\(^2\). Unlike their rural conspecifics which specialize in voles, urban Kestrels are generalists, preying on passerines and mammals, but also reptiles and insects. We explore this alternative diet through pellet analyses along an urbanization gradient over a 5-year period and link diet to reproductive performance, taking local weather conditions into account.

**Results:** Our results showed that weather had a greater influence on breeding performance than did diet. Warm and dry weather during the arrival and courtship period was correlated with earlier egg-laying, higher nestling survival and an overall higher breeding success. Dry winters increased the proportion of mammalian prey, whereas low temperatures and high rainfall during the nestling phase increased the proportion of avian prey. Overall, a more diverse diet was also associated with higher rainfall, but only during the arrival and courtship period.

**Conclusion:** Our research shows a stronger connection between breeding performance and weather conditions than between breeding performance and diet composition, although there may be indirect effects of weather on prey availability which augment the impact of diet on reproductive output in the Eurasian Kestrel.

Urbanization is a global anthropogenic phenomenon which results in the increase of impervious surfaces, the loss of green space and high turnover of species composition (Ramalho & Hobbs 2012). Among birds, urbanization can result in a population decline for many species (Sol et al. 2014), while others benefit from the altered conditions which may increase availability of food and nest sites (Rodewald & Bakermans 2006, González-Oreja 2011). Blair (1996) categorized bird communities along urban gradients and defined ‘urban avoiders’, which are restricted to their native, undisturbed habitats, and on the contrary a small number of ‘urban exploiters’, which are often non-native (Jokimäki & Suhonen 1998) and very successful in urbanized, human-dominated environments. This division within avian communities is defined as ‘biotic homogenization’, a phenomenon linked to global urbanization processes (Blair 2001, McKinney 2006). More than 25 avian raptor species have been recorded worldwide in urban settings (Love & Bird 2000). High food availability within urban settings can lead to positive population responses in predatory birds (Chace & Walsh 2006). In particular, specialized bird-feeders like the Goshawk *Accipiter gentilis*, the Sparrowhawk *Accipiter nisus* or some falcon species respond well to urban landscapes because of the large biomass of avian prey (Newton 1980, Cade et al. 1996, Berry et al. 1998, Kenward 2006, Suri 2016). Some raptor species extend their home ranges beyond urban boundaries (Chace & Walsh 2006) and breed in inner-city districts while hunting in rural areas (Riegert et al. 2007).
This strategy might be limited to smaller cities and appears difficult in larger urbanized areas (Sumasgutner et al. 2014a).

The Eurasian Kestrel *Falco tinnunculus* (hereafter Kestrel) is known to have inhabited and bred in urban environments since at least the second half of the 19th century (Cramp & Tomlins 1966). Studies on this species have been conducted in several European cities, for example Bratislava (Darolová 1992), Warsaw (Rejt 2001), Rome (Piattella et al. 1999) and several cities in Israel (Charter et al. 2007). Drawing general conclusions on the status of urban Kestrels remains difficult, as each city presents unique qualities in terms of size (which affects distances to potential rural hunting grounds), building structure (abundance of suitable nest sites), the composition of vegetation and amount of urban green space (which influences availability of prey). In Vienna, Austria, the population density of Kestrels is especially high not only compared to other European cities but also when compared to rural areas (Gamauf 1991, Kostrzewa & Kostrzewa 1993, Sumasgutner et al. 2014a). Because of the Kestrels’ inability to construct nesting platforms, building cavities provide attractive breeding sites (Village 1990). In particular, roof openings, which are characteristic of Vienna’s historical city centre, are well sheltered and are therefore preferred over open nest sites (Sumasgutner et al. 2014b). Kestrels are not true ‘urban exploiters’ though – apart from using artificial breeding sites, they do not profit from other resources related to urban environments. On the contrary, their breeding success, measured through lower hatching rates and fledged brood sizes, actually decreases with increasing urbanization towards the city centre (Sumasgutner et al. 2014a). Similar observations were reported for passerine birds in urban environments (Chamberlain et al. 2009).

To settle successfully in an urban habitat, an appropriate food supply is one of the most important requirements (Witt 2000). While their rural conspecifics specialize in hunting small rodents, especially voles, urban Kestrels are generalists, preying not only on mammals, but also largely on birds (Galanos 1991, Piattella et al. 1999, Salvati et al. 1999, Kübler et al. 2005, Sumasgutner et al. 2013) and even on reptiles and insects (Riegert et al. 2009, Sumasgutner et al. 2013). The amount of avian prey, mainly passerines, increases with increasing urban cover and can even become the predominant prey in city centres (Kübler et al. 2005, Sumasgutner et al. 2013, Sumasgutner et al. 2014b). Most rodent species inhabiting Vienna are nocturnal (Mitter et al. 2015) and therefore inaccessible to a diurnal raptor like the Kestrel. A rodent survey in Vienna in 2010 showed almost exclusively field mice of the genus *Apodemus* (98.4% of trapped species were Wood Mouse *Apodemus sylvaticus*, Yellow-necked Mouse *Apodemus flavicollis* and Pygmy Field Mouse *Apodemus uralensis*), as main potential prey available within urban parks (Sumasgutner et al. 2014a). However the distances to suburban areas, where these diurnal rodents would be available, are long for inner-city breeding pairs. It therefore seems more efficient for urban Kestrels to hunt within a smaller home range (Sumasgutner et al. 2014a) and shift to alternative prey available in closer proximity to the nest site.

Besides the impact of the urbanization gradient on diet, there might also be a strong connection between diet composition and weather conditions, both of which influence the breeding phenology of a predatory bird. For example, in Fenno-Scandinavia, prey availability follows a distinct 3–4-year vole-cycle (Hansson & Henttonen 1985, Korpimäki et al. 2005), strongly affecting Kestrels’ breeding performance. During phases of high vole abundance, the egg-laying starts earlier, clutch sizes are larger and the number of fledged offspring is higher than in low vole years (Korpimäki & Wiehn 1998, Valkama et al. 2002). Due to fluctuating food conditions, raptors might be forced to switch to alternative prey items. This might affect specialist predators more than generalist predators due to their different foraging efficiencies (Terraube et al. 2011). This might also be true on an individual level. A shift in diet composition is one of the most pronounced characteristics of urban Kestrels, and inner-city Kestrels are considered to be generalists compared to their rural counterparts. In spite of their broad diets, overall foraging efficiency was hypothesized to be low for Viennese Kestrels and starvation of chicks was named among the main causes for the observed decreased breeding success in inner-city pairs (Sumasgutner et al. 2014a). On the other hand, a more heterogeneous habitat, such as a patchy urban environment, might also have the potential to buffer adverse weather conditions by providing a more diverse diet through the higher availability of alternative prey species. A wider diet breadth or alternative diet composition might positively affect the health status of the nestlings (see, e.g., Sternalski et al. 2012, Hegemann et al. 2013). Diet composition is therefore an important determinant of success for an urban breeding raptor, and it may be strongly linked with local weather conditions.

This study aimed to identify the relationship between reproductive success of Kestrels and (i) an alternative diet composition associated with urbanization, (ii) local
weather conditions and (iii) nest site features (i.e. location along the urban gradient and nest type) over a 5-year period (2010–14). We expect to find a link between the altered conditions in the urban habitat and Kestrels’ breeding performance (Sumasgutner et al. 2014a, 2014b) and predict that the proportion of avian prey increases from the periphery to the city centre while productivity decreases. At the same time we predict a strong connection between diet composition and local weather conditions. We expect inner-city birds to perform better during adverse conditions due to more stable prey availability, while more suburban birds on the city outskirts, that rely mainly on voles and breed in open nest sites instead of building cavities, are expected to perform poorly in cold and rainy weather.

Material and methods

Study species

The Kestrel is the most abundant raptor in Vienna, Austria (48°12'N, 16°22'E; 415 km², approximately 150–500 m above sea level, 1.8 million inhabitants; Statistik-Austria 2016). Kestrels are capable of breeding in various habitats as long as open landscapes are available for hunting (Village 1990). Kestrels return to the inner-city of Vienna in February/March (Sumasgutner et al. 2014b). The role division during reproduction follows the usual scheme for raptors (Newton 1979): the male provides most of the prey for the female and offspring while the female performs most of the incubation, brooding and nest guarding. The most commonly used nest types in the city of Vienna are building cavities, especially roof openings, as well as planters, nest-boxes and abandoned corvid nests (Sumasgutner et al. 2014b).

The urbanization gradient

The urbanization gradient indicates the change in the percentage of sealed soil with increasing distance from the centre to the periphery and is connected to differences in space utilization, building density and housing structure, proportion of vegetation and level of anthropogenic disturbance. We calculated levels of urbanization for the study site in Vienna in ArcGIS 10, defining it as land covered by buildings and traffic areas on a land allocation map (digitized in 55 categories of land use between 2007 and 2010, scale 1:7500, resolution 150 mm), in a circle of radius 500 m around the nest sites, sensu Zuckerberg et al. (2011). Areas with <1% of sealed soil were defined as rural and excluded from the analysis. Excluding these surroundings, mostly forested and agricultural areas, the urban study area covered 243 km². The 56 nests used in this study ranged between 26% (most suburban) and 97% (most urban) of sealed soil.

Breeding parameters

Occupied nests that were accessible via an attic or by facade and tree climbing were monitored four to six times during each breeding season to determine: (1) the laying date, (2) the clutch size, (3) the number of hatched offspring and (4) the number of fledged young. In total, 56 broods were examined between 2010 and 2014. The laying date was estimated either through direct observations or by subtracting 30 days from the estimated date of hatching based on morphometric measurements of the chicks (Kostrzewa & Kostrzewa 1987). Assuming a laying interval of two days, the laying date of the first egg can be estimated, given that incubation among Kestrels starts usually at the third egg and chicks hatch about 30 days later (Village 1990). During repeated monitoring, the nestlings were measured, weighed and ringed (with rings from the Ringing Centre Radolfzell, Germany) when they were at least ten days old (wing length ≥54 mm). The lengths of the culmen, tail, wing, tarsus, claws and feet (Eck et al. 2011) were measured for age determination (Kostrzewa & Kostrzewa 1993). The final inspection took place in the last week of the nestling period (24–30 days after hatching). Nestlings fledge after 28–31 days (Village 1990); hence we considered pairs successful if they produced at least one 28-day-old chick. The size of the fledged brood was the number of nestlings in successful nests at week 4.

Pellet analyses

Pellets, plucked feathers and prey remains (n = 627) were collected from the nest sites between 2010 and 2014 by taking one third of the nest’s content crosswise at each nest visit between hatching and fledging. Nest cavities are usually empty after the chicks fledge (due to limited space and a completely open front); nest-boxes still containing pellets after fledging were cleaned after the season by their private owners. Fresh remains that still had a nutritional value were identified on site and excluded from the analysis. Excluding these remains, mostly voles, pellets were repeatedly investigated in two different study
years). The pellets were dissected and prey remains classified as ‘mammals’, ‘birds’, ‘reptiles’ or ‘insects’. We identified prey to species or genus level where possible with the aid of reference collections at the Museum of Natural History, Vienna. We assessed the minimum number of each category of prey per pellet: largest number of different jaws, upper or lower mandibles, skulls or pairs of incisors in small mammals; plugged feathers in birds; pairs of mandibles, tarsi or ovipositors in insects. Estimates of biomass (g) were made as follows: 18.8 g for small mammals, 22.4 g for sparrow-sized birds, 76.4 g for thrush-sized birds, 330 g for pigeons, 10 g for reptiles, 1.5 g for Orthoptera and 0.2 g for Coleoptera (Glutz von Blotzheim & Bauer 1980, Arroyo 1997).

Diet breadth (B) was calculated according to Levin’s index (Levins 1968) as \[ B = \sum_p i \cdot p_i^2; \] where \( p_i \) is the proportion of the diet represented by prey type \( i \). As variables were not normally distributed, nonparametric tests were used for analysis. To receive values between 0 and 1 we used the standardized Levin’s index (Krebs 2004): \[ B_k = \frac{(B−1)}{(N−1)}, \] with \( N \) defining the number of different prey categories. Higher values reflect higher diet breadth, and so more diverse prey consumption.

**Weather conditions**

Meteorological stations in Vienna are operated by Zentralanstalt für Meteorologie und Geodynamik. Data were provided from two stations: ‘Vienna inner-city’ (1.3 km from the centre) and ‘Vienna Donaufeld’ (6.7 km from the centre), covering the time period of March 2010–August 2014. Each nest site was allocated to the closest weather station. Air temperature and rainfall were expressed in five different values: \( \text{MaxT} = \) average maximum temperature; \( \text{MinT} = \) average minimum temperature; \( \text{Rain} = \) sum of rainfall; \( \text{RainD} = \) number of rain days and \( \text{RainI} = \) intensity of rain, meaning sum of rainfall per rain day. For each nest site these variables were assigned for four different time periods: winter (December, January and February before breeding), arrival and courtship (March until laying date), incubation (from laying date until hatching, four calendar weeks) and nestling period (from hatching until fledging, four calendar weeks). These periods are dependent on the laying date and therefore different for each nest site. We provide an overview in weather data for all breeding seasons as supplementary material 1. To reduce the number of different weather variables per time period and assure of them being uncorrelated, a principal component analysis (PCA) was performed. The PCA produced two principal components (hereafter PC) for each time period with an Eigenvalue > 1 and explaining between 83.8% and 94.5% of variance (supplementary material 2).

**Statistical analysis**

All statistical analyses were performed with the software R version 3.2.3 (R Development Core Team 2015). The confidence intervals were set at 95% (corresponding to a significance level of \( P = 0.05 \)) for all tests conducted. Descriptive statistical values are given as mean ± se.

**Breeding performance, weather conditions and diet composition**

To evaluate the impact of nest site features, local weather conditions and diet composition on breeding parameters, we built generalized linear mixed effects models (GLMMs) and linear mixed effects models (LMMs) for the timing of breeding using the ‘lme4’ package (Bates et al. 2014). Nest site ID and study year were included as random factors to avoid pseudoreplication (Hurlbert 1984). Nest site ID controlled for a lack of independence of broods fledged from the same site. Year controlled for broods fledged in the same year. All explanatory variables were centred and scaled beforehand to ensure that effect sizes were on a comparable scale. We then tested for correlations between fixed effects using Spearman’s rank correlation coefficient (\( r_s \)). A set of candidate models was fitted (supplementary material 3) and each candidate model was compared to one another using Akaike Information Criterion values, corrected for small sample size (AICc) in the package ‘AICcmodavg’ (Mazerolle 2014). We considered as the final model the one with the minimum AICc value (Burnham et al. 2011). Residual distributions of all models were inspected to assess model fit. We used the ‘MuMIn’ package (Barton 2014) to compute \( R^2 \) for GLMMs and LMMs. We present the conditional \( R^2 \) (variance explained by both fixed and random factors) in the results section. The error distribution was chosen according to the response variable. To examine breeding parameters we used a Poisson distribution and log link function to determine the dependence of clutch size/nest site and number of fledged offspring/nest site, we used a binomial distribution and logit link function for the hatch-fledge ratio/nest site and a Gaussian distribution and identity link function for laying dates (expressed as Julian day of egg-laying)/nest site. The hatch-fledge ratio was set using the ‘cbind’ function with the number of hatched offspring as binomial denominator. We fitted weather conditions (generated PC scores), diet composition (proportion of
mammals, proportion of birds or Levin’s standardized index), the urbanization gradient and the nest types (building cavity, \(n = 35\); nest-box, \(n = 7\); planter, \(n = 10\) or corvid nest, \(n = 4\)) as fixed effects. For all breeding parameters we also controlled for the laying date (centred to the mean of the study year). The diet parameters and the urbanization gradient were correlated (proportion of mammals in diet versus urban gradient \(r_s = -0.28, P = 0.04\); proportion of birds versus urban gradient \(r_s = 0.30, P = 0.03\)), hence we used the interaction terms of these variables. We indicated these interaction terms with the abbreviations ‘M:UG’ for mammals and ‘B:UG’ for birds. We fitted either the urbanization gradient or the different nest types to account for their correlation (\(r_s = -0.44, P \leq 0.001\)). To disentangle the relationship between nest types and breeding parameters we performed post-hoc comparisons of all factor levels using the package ‘lsmeans’ (Lenth & Hervé 2015).

**Diet composition and weather conditions**

Another set of GLMMs was fitted to analyse the dependence of diet composition on weather conditions, using all PC representing weather data as well as laying date and the urbanization gradient as fixed effects. According to the response variables, which ranked between 0 and 1 (proportion of mammals or birds in diet and Levin’s standardized index), the error distribution was chosen as binomial and models were fitted with the logit link function. See supplementary material 3 for the full candidate model list. Weather data (PC scores) of different time periods separately and the urbanization gradient were tested. We did not fit the lay date in these models because of the strong correlation with several PC scores (lay date and PC1winter: \(r_s = -0.44, P \leq 0.001\); lay date and PC1court: \(r_s = 0.91, P \leq 0.001\)).

**Ethical note**

The study was performed under license of the Environmental Protection Bureau of Vienna (MA22/1263/2010/3), the Ministry for Science and Research (BM.WF-66.006/0021-II/3b/2013) and the ethics committee of the University of Veterinary Medicine, Vienna (BGBl.Nr.501/1989i.d.g.F.). All data were acquired following current Austrian and EU law as well as the Weatherall Report and the guidelines for treatment of animals in behavioural research and teaching (ASAB 2012).

**Results**

**Diet composition**

A minimum number of 1140 single prey items was identified out of 627 pellets, plucked feathers and other prey remains; see supplementary material 4 for a full list of identified prey items. The main prey categories were mammals and birds, based on the estimated biomass of prey items. In three years avian prey was of higher importance than mammalian prey (2010: 47.3%, 2012: 53.6% and 2013: 50.1%). In 2011 pellets consisted of 58.1% mammals and 36.3% birds; while in 2014, pellets consisted of 75% mammals and 15.9% birds (Figure 1). The average yearly contribution of reptiles ranged between 3.8% (2012) and 10.8% (2013) and the least represented group were insects (<1%). The determined standardized Levin’s index of diet breadth (\(B_A\)) ranged between 0 and 0.6, where higher values reflect a more diverse diet.

Regarding the studied breeding seasons separately, 2013 revealed the highest diet breadth compared to all other years; 2014 had the lowest \(B_A\) (Figure 2). A relatively high amount of reptiles in diet composition was the best predictor for a high Levin’s index (\(r = 0.45, P \leq 0.001\)). A total of six nest sites had a diet composition of 100% mammals, five of them were found in 2014. Avian prey was above 93% at two nest sites in 2010 and 2012, respectively. The highest prey diversity was found in 2013 in a nest with 37.2% mammals, 42.8% birds, 19.1% reptiles and 0.99% insects.

**Breeding parameters**

In 2014, both the earliest (31 March) and the latest egg-laying date (24 May) were recorded. In contrast, the
breeding pairs studied in 2013 started egg-laying within a period of 15 days (between 3 and 17 May). The 2014 breeding season showed the overall highest breeding success (mean clutch size = 5.5 ± 0.2 eggs per pair, number of hatched offspring = 4.8 ± 0.3 and number of fledged young = 4.3 ± 0.3), whereas the smallest mean clutch size (4.3 ± 0.3) and lowest mean number of hatched offspring (3.4 ± 0.3) were found in 2013, and the lowest mean number of fledged young (2.2 ± 0.4) in 2010. Closed nest structures had larger mean clutches than open nests (5.0 ± 0.1 eggs for building cavities; 5.0 ± 0.3 for nest-boxes; 3.0 ± 0.6 for crow nests, but 5.3 ± 0.3 for open planters). The mean number of fledged offspring was highest for broods in nest-boxes (4.0 ± 0.4), planters (3.9 ± 0.3) and building cavities (3.0 ± 0.3), whereas the lowest mean was found in crow nests with 0.8 ± 0.8 (Figure 3).

**Weather conditions**

For two time periods (‘arrival and courtship’ and ‘nestling’) the highest maximum air temperatures (16.9 ± 0.4°C and 28.1 ± 1.4°C, respectively) were reached in 2012. In 2014 the lowest minimum air temperature was reached during the incubation and nestling period (11.1 ± 1.4°C and 14.4 ± 1.5°C, respectively; supplementary material 1.2). The total amount of rainfall was highest in 2010 (397.5 mm), but 2013 had the highest rainfall during the nestling period (82.6 mm; supplementary material 1.3).

**The relationship between nest site features, weather conditions, diet composition and breeding parameters**

Table 1 gives an overview on final candidate models, LMMs for lay date and GLMMs for clutch size, number of fledged young and hatch-fledge ratio, including nest site features and weather conditions as fixed effects. Diet parameters did not feature in the best model and were dropped during the model selection process. The $R^2$ values for the explanatory capacity of the models differed between 95% for lay date and 3% for clutch size. Warm and dry arrival and

| Table 1. Final models presenting the dependence of breeding parameters on nest site features (Figure 4, left panel) and weather conditions (Figure 4, right panel). Diet parameters did not feature in the best model and were dropped during the model selection process. The dependence of clutch size, number of fledged young and hatch-fledge ratio were analysed in generalized linear mixed effects models (GLMM), or linear mixed effects models (LMM) for lay date ($n$ = 56 nest sites). Fixed effects: nest type or urbanization gradient and PC1/PC2 – first/second principal components for concerned time periods; factors with highest loadings for pc scores are given in brackets: $r$ – total rain, $r_d$ – number of rain days, $r_i$ – intensity of rain, $t_{(max)}$ – maximum air temperature and $t_{(min)}$ – minimum air temperature. |
|--------------------------------------------------|-------------------|----------------|--------------|
| Lay date                                         | $\chi^2$ | df | $P$ | $R^2$ | Figure 4 |
| Nest type                                        | 17.98    | 3 | 0.001 | a         |
| PC1courtship (+$r$, +$r_d$, +$t_{(min)}$)        | 282.13   | 1 | 0.001 | b         |
| PC2courtship (+$t_{(max)}$, -$r_i$)              | 39.09    | 1 | 0.001 | c         |
| Intercept                                        | 721.68   | 1 | 0.001 |            |
| Clutch size                                      | 1.47     | 1 | 0.2252 |          |
| PC1winter (-$r$, -$r_d$, -$r_i$)                 | 690.57   | 1 | 0.001 |          |
| Intercept                                        | 1.04     | 1 | 0.3720 |          |
| Number of fledged young                          | 7.45     | 3 | 0.059 | d         |
| Nest type                                        | 5.79     | 1 | 0.016 | e         |
| PC1winter (-$r$, -$r_d$, -$r_i$)                 | 192.00   | 1 | 0.001 |          |
| Intercept                                        | 1.04     | 1 | 0.3720 |          |
| Hatch-fledge ratio                               | 0.80     | 1 | 0.0674 | g         |
| Urbanization gradient                            | 3.34     | 1 | 0.001 | h         |
| PC1courtship (+$r$, +$r_d$, +$t_{(min)}$)        | 16.41    | 1 | 0.001 | i         |
| PC2courtship (+$t_{(max)}$, -$r_i$)              | 8.00     | 1 | 0.0047 |          |
courtship periods correlated with earlier egg-laying (Figure 4(b and c)), high temperatures and low rain intensity during the arrival and courtship period were also associated with higher chick survival in the nest (hatch-fledge ratio, Figure 4(g and h)). Overall, dry winters also resulted in higher breeding success (number of fledged offspring, Figure 4(e)). Post-hoc comparisons showed that the significant influence of nest type on the lay date was only due to an earlier egg-laying in building cavities and later egg-laying in planters (lsmeans: estimate $-6.39 \pm 1.71$, t-ratio = $-3.74$, $P = 0.0025$). The number of fledged young was

Figure 4. Breeding performance (Julian day of egg-laying (a–c), number of fledged offspring (d–e) and hatch-fledge ratio (f–h); plus CI 95%) of Eurasian Kestrels in dependence of nest site characteristics (left side) and weather scores (right side). Model details are given in Table 1; black bars on the x-axis represent sample size.
significantly higher in building cavities than in crow nests (lsmeans: estimate 1.58 ± 0.58, z-ratio = 2.70, \( P = 0.0347 \)).

**Weather effect on diet composition**

Table 2 gives a summary of the final models (GLMMs) describing the dependence of diet parameters on weather conditions. Differences in diet composition depended highly on the total amount of rain and the number of rain days during the arrival and courtship period. More precipitation led to a higher diet breadth (Levin’s index) during the following breeding season. Dry winters increased the proportion of mammalian prey, whereas low temperatures and high rainfall during the nestling phase increased the proportion of avian prey. Breeding pairs nesting closer to the city centre fed slightly more on birds than those located on the periphery, however, this relationship was not statistically significant.

**Discussion**

Our study showed the influences of diet and weather on reproductive success to be highly entangled. Weather conditions have an obvious direct effect on breeding performance but also an indirect influence through the seasonal effect on prey availability and thus diet composition. Our findings show that local weather conditions are important in explaining differences in productivity of the Viennese Kestrel population. In particular, the weather during the period before egg-laying (winter, arrival and courtship) seems to be important in determining breeding performance, potentially due to earlier egg-laying under warm and dry conditions. Clutch size was the breeding parameter least affected by weather conditions. However, the number of fledged young was significantly higher during mild winters, which was not a carryover effect of already smaller clutches. This implies that warm and dry conditions during the early breeding phase positively influence productivity. There is evidence that environmental variation during early-life (Lindström 1999) might even induce life-history effects. For example, Herfindal et al. (2015) found a correlation between warmer temperatures during the nestling period and reduced future lifetime reproductive success in Goshawks. Similarly, Sumasgutner et al. (2016) found future recruitment probability of offspring to be influenced by weather conditions experienced on the nest. The direction of this correlation was different in two colour morphs of Black Sparrowhawks *Accipiter melanoleucus*, which might relate to different prey provisioning rates under different light or weather conditions (Tate et al. 2016). These findings underline again the important interplay of prey and weather in influencing the long-term fitness of raptors.

We expected to find a link between altered conditions in the urban habitat and Kestrel breeding performance (Sumasgutner et al. 2014a, 2014b). Other falcon species, for example Peregrine Falcons *Falco peregrinus*, American Kestrels *Falco sparverius* and Lesser Kestrels *Falco naumanni*, but see also the case in Tella et al. (1996), are known to experience increased productivity in urban habitats (Chace & Walsh 2006). One reason might be that they are not specialized in hunting small mammals like the Eurasian Kestrel, but adapted to avian prey or insects as their main diet, both of which may be abundant in urban areas. Optimal foraging theory (Stephens & Krebs 1986) predicts that the occurrence of types of prey in a diet is proportional to their profitability. The longer the distance to the hunting ground, the more profitable the prey must be to justify the effort. The alternative prey hypothesis states that a predator with a strong preference for a particular type of prey will switch to an alternative prey only when the main prey is scarce (Lack 1954). This hypothesis was tested in systems where prey availability fluctuates between years, but could also apply to the trade-offs faced by Kestrels (defined by nutritional value and hunting effort) along an urbanization gradient in Central Europe (Sumasgutner et al. 2014a, 2014b). The main prey of Kestrels are voles, which are of higher nutritional value and easier to catch with the Kestrels’ typical hunting technique of hovering and dropping than common alternative prey.

**Table 2.** Final models presenting dependence of different diet parameters on nest site features and weather conditions. The dependence of the proportion of mammals or birds in the diet and the Levin’s index of diet breadth were analysed using generalized linear mixed effects models (GLMM; \( n = 56 \)). Fixed effects: nest type and PC1/PC2 – first/second principal components for concerned time periods; factors with highest loadings for pc scores are given in brackets: \( r \) – total rain, \( t_d \) – number of rain days, \( t_r \) – intensity of rain, \( t_{(max)} \) – maximum air temperature, and \( t_{(min)} \) – minimum air temperature.

|                          | \( \chi^2 \) | df | \( P \)  | \( R^2 \) |
|--------------------------|-------------|----|---------|---------|
| Levin’s index of diet breadth |             |    |         | 0.61    |
| PC1courtship \( (+r, +t_d, +t_{(min)}) \) | 10.00       | 1  | 0.0016  |         |
| PC2courtship \( (+t_{(max)}, -t_r) \) | 3.74        | 1  | 0.0532  |         |
| Intercept                | 15.53       | 1  | ≤ 0.0001|         |
| Mammals in diet          |             |    |         | 0.14    |
| PC1winter \( (-r, -t_r, -t_d) \) | 5.63        | 1  | 0.0177  |         |
| Intercept                | 0.00        | 1  | 0.9666  |         |
| Birds in diet            |             |    |         | 0.28    |
| Urbanization gradient    | 1.59        | 1  | 0.2067  |         |
| PC1nest \( (-t_{(max)}, -t_{(min)}, +r, +t_d) \) | 4.15        | 1  | 0.0416  |         |
| Intercept                | 10.05       | 1  | 0.0015  |         |
species, such as passerine birds (Kirkwood 1979, Steen et al. 2012). In the urban setting of large metropolises, Kestrels have to fly long distances to hunt voles. Due to the effort involved in travelling such distances, they switch to prey items which are more readily available within the inner-city districts, such as passerines, which are of a similar size but with poorer nutritional value. In this study, however, we did not observe such a strong effect of the urbanization gradient on the relative proportions of alternative prey items within the diet. It might be that prey composition was not accurately estimated, since certain prey categories might be completely digested, leaving no remains (Trierweiler & Hegemann 2011). This might lead to an overestimation of mammalian prey and an underestimation of birds (plucked outside the nest) and invertebrates (Düesberg 2012). A complete quantitative assessment of diet is not possible with pellet analyses alone. Other techniques, such as video-monitoring, are also possible, and have been used in a previous study, but such techniques can limit the sample size tremendously (Sumasgutner et al. 2014b).

Finally, we expected to find an indication that a stable and reliable avian prey supply in urban habitats can buffer against adverse weather conditions, allowing Kestrels to perform better under cold and rainy weather compared to typical vole-hunters. We found a more diverse diet (higher Levin’s index) under wetter weather conditions during the arrival and courtship period. In the same weather conditions, we also witnessed an increase in the hatch-fledge ratio, indicating the suggested indirect positive influence of a diverse diet on nestling survival. Since precipitation is known to decrease prey activity (Brown 1956), as well as the hunting activity of Kestrels (Rijnsdorp et al. 1981), foraging success is expected to be lower in rainy conditions. Consequently, we expect reduced feeding rates of nestlings and lower chick survival in rainy weather. In urban environments, where Kestrels are able to prey on a wider variety of species, this impact might be reduced.

To conclude, our results showed a stronger connection between breeding performance and weather conditions than between breeding performance and diet composition, although one has to assume indirect effects of weather on prey availability. Particularly warm and dry winters before arrival and courtship periods had a positive influence on the proportion of small mammals in the diet and on breeding success in the Kestrel. Additionally, we found an effect of the nest site structure, which was correlated with the urbanization gradient, on the timing of breeding and reproductive success.

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ORCID

H. W. Krenn http://orcid.org/0000-0003-4323-5099
P. Sumasgutner http://orcid.org/0000-0001-7042-3461

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