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of the Eurasian Kestrel (*Falco tinnunculus*)
in human altered landscapes“

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Costs and benefits in the settlement decisions of the Eurasian Kestrel (*Falco tinnunculus*) in human altered landscapes

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This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Sumasgutner P, Nemeth E, Tebb G., Krenn HW, Gamauf A (*accepted*) 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*.
- II Sumasgutner P, Schulze CH, Krenn HW, Gamauf A (2014) Conservation related conflicts in the nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey. — *Landscape and Urban Planning* 127:94-103.
- III Sumasgutner P, Krenn HW, Duesberg 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.
- IV Sumasgutner P, Rubin I, Gamauf A (2014) Collecting blood samples in Eurasian Kestrels (*Falco tinnunculus*) (Aves: Falconidae) via blood-sucking bugs (Insecta: Hemiptera: Reduviidae) and their use in genetics and leucocyte profiles. — *Annalen des Naturhistorischen Museums Wien, B* 116:247-257.
- V Preliminary results: Genetic variability in Eurasian kestrels (*Falco tinnunculus*) in Vienna, Austria.
- VI Sumasgutner P, Vasko V, Varjonen R, Korpimäki E (*submitted*) Public information revealed by prey remains in nest-sites is more important than ectoparasite avoidance in the settlement decisions of Eurasian kestrels (*Falco tinnunculus*). — *Behavioral Ecology and Sociobiology*.

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Summary

The Eurasian kestrel (*Falco tinnunculus*) is a widespread species of raptor that is frequently seen hunting in open landscapes. It breeds in various habitats, including highly urbanized areas. The flexibility in the choice of breeding grounds makes the species ideal for studies of the relative costs and benefits of settling in the city or in the suburbs.

At the start of my PhD work I initiated the 'Vienna kestrel project' in an attempt to understand the high breeding density of kestrels in the centre of Vienna, Austria. Between 2010 and 2012 I monitored a substantial proportion of the urban kestrel population, simultaneously collecting data on the composition of the landscape and the structure of buildings at the nest sites. I used the varying extent of sealed soil between the city centre and the peripheral areas to define an urban gradient and related all breeding parameters to this environmental scale. The focus of the work was to investigate whether kestrels are attracted to the city centre by favourable living conditions, such as the ready availability of suitable nest sites or good levels of potential prey, or are pushed out of rural areas by unfavourable conditions there. The breeding data were analysed with regard not only to the habitats and nest sites chosen by the birds but also to the availability of prey and the composition of the birds' diets. We performed a survey of small mammals in Vienna (Chapter I) and as part of a long-term collaboration with BirdLife Austria we collected data on the abundance of prey-sized birds in urban Vienna (Chapters I, II).

The results showed that high breeding densities in urban habitats do not necessarily correlate with high quality of the habitat, either in terms of prey availability or with regard to the reproductive success of the birds that nevertheless choose to breed in the city centre (Chapter I). A comparison of breeding sites (landscape composition and building structure) with random control points revealed that birds in the centre benefit from the presence of more cavities suitable for breeding but suffer from having to fly further to their hunting grounds (Chapter II). The lack of large open green spaces in the centre, combined with the lower availability of diurnal rodents, leads to a shift in the main categories of prey from small mammals in the periphery to avian prey in the centre. The shift was demonstrated by analysis of the birds' pellets (Chapter I, III) and the results were confirmed by video monitoring of selected nests (Chapter II).

In the second (still unpublished) part of the 'Vienna kestrel project' I collected data on the condition of the chicks. I used morphometric measurements to derive a body condition index, recorded carotenoid levels (data not shown), counted cases of infestation with ectoparasites and blood parasites, recorded heterophil/lymphocyte ratios (Chapter IV) and undertook genetic

work to use genetic heterogeneity (Chapter V) to differentiate between quantity (breeding success) and quality of nestlings.

The work required a number of methodological developments. In rural areas kestrels may be trapped in nest-box traps or using baited bal-chatri traps but these methods are hardly suitable for use in an urban setting. I thus collected blood samples from incubating birds non-invasively by taking advantage of blood-sucking bugs. In Chapter IV I present an evaluation of the use of blood samples collected in this manner for calculating various indexes of the birds' condition. I cross-amplified microsatellite markers initially established for *F. peregrinus* and *F. naumanni* to study genetic heterogeneity (preliminary results in Chapter V). We are currently analysing the data to determine the frequency of extra-pair copulations in highly urbanized areas and are applying a landscape genetics approach to study genetic differences. The results will be submitted for publication within the next few months.

For the final part of my PhD (Chapter VI) I was granted access to a long term data-set of settlement decisions for kestrels in a Finnish population. In an experimental nest-box setup, breeding cavities were randomly cleaned of pellets and other prey remains or left un-cleaned. The experiment was undertaken to assess the use of public information in the settlement decision: prey remains represent a visual sign of previous breeding success at the site. The non-random distribution of breeding kestrels in my urban study system could in principle be partially explained by the use of public information or by conspecific attraction. The field experiment allowed these possibilities to be distinguished. I complemented the existing study of the Finnish research team by testing the 'ectoparasite avoidance hypothesis', which predicts different results from those predicted by the public information hypothesis. We found that kestrels first occupied un-cleaned nest boxes: eggs were laid earlier in un-cleaned nest boxes than in cleaned ones. This confirms that remains of prey are indeed used as public information. Nevertheless, breeding in un-cleaned nest boxes was connected to higher levels of infestation of young nestlings with ectoparasites, indicating that the settlement decision is associated with some costs. The breeding success, calculated as the total number of fledglings, was equal for un-cleaned and cleaned nest boxes.

In conclusion, although kestrels are city-dwelling raptors and the species seems to be exploiting the urban environment, it does not profit from highly urbanized areas and does not breed more successfully in the centre of cities. The finding is problematic for conservation measures and is indicative of the emergence of an ecological trap. Finally, by means of an experimental approach I was able to substantiate the use of public information in the settlement decision of Eurasian kestrels.

Zusammenfassung

Der Turmfalke (*Falco tinnunculus*) ist ein anpassungsfähiger Greifvogel, der viele anthropogene Lebensräume erschlossen hat, einschließlich stark urbanisierter Gebiete. Diese Plastizität in der Nistplatzwahl ermöglicht es uns, den Turmfalken als Modellart für eine Kosten-Nutzen Analyse heranzuziehen und Konsequenzen der Nistplatzwahl zwischen innerstädtischen und suburbanen Brutvögeln zu vergleichen.

Im ersten Teil meiner Doktorarbeit habe ich das "Turmfalkenprojekt Wien" initiiert. Dessen Forschungsziel war es, die hohe Brutpaardichte von Turmfalken in der Wiener Innenstadt zu erklären. In einem Monitoring in den Jahren 2010 bis 2012 wurden städtische Turmfalken erfasst und die Habitatcharakteristiken sowie die Gebäudestruktur der gewählten Nistplätze erhoben. Zu diesem Zweck wurde ein Urbangradient auf Basis der zunehmenden Flächenversiegelung vom Stadtrand in die Innenstadt definiert. Der Bruterfolg wurde mit dem Urbangradient verschnitten, um die Erfolgsstrategien urbaner Turmfalken zu erforschen. Die wesentliche Forschungsfrage war, ob Turmfalken von vorteilhaften Lebensbedingungen, wie höherer Nistplatz- oder Beuteverfügbarkeit in die Innenstadt angezogen werden, oder ob das Gegenteil der Fall ist, nämlich dass Turmfalken aufgrund nachteiliger Lebensbedingungen zu einer Landflucht veranlasst werden. Dazu wurde der Bruterfolg nicht nur mit der Habitatausstattung und der unmittelbaren Gebäudestruktur verschnitten, sondern auch mit Beuteverfügbarkeit und Nahrungswahl. Dazu haben wir ein Kleinsäugermonitoring (Kapitel I) sowie im Rahmen einer langjährigen Kooperation mit BirdLife Österreich ein Brutvogelmonitoring zur Erfassung der Kleinvögel durchgeführt (Kapitel I, II).

Die hohe Anzahl an Brutpaaren im städtischen Raum korreliert nicht mit höherem Bruterfolg. Die Dichte selbst (*nearest-neighbourdistance*) konnte den abnehmenden Bruterfolg nicht erklären, sehr wohl aber die höhere Flächenversiegelung (Kapitel I). Der Vergleich zwischen den Brutplätzen und Zufallspunkte zeigte einen *trade-off* zwischen mehr Brutnischen im städtischen Raum, doch längeren Jagddistanzen zu größeren Grünflächen (Kapitel II). Das Fehlen von großen Grünflächen im Stadtzentrum, zusammen mit der geringeren Verfügbarkeit von tagaktiven Nagern als Beutetiere, führt außerdem zu einer Verschiebung der Hauptbeutekategorien: In der Peripherie werden hauptsächlich Kleinsäuger gejagt, wohingegen im Stadtzentrum der Anteil an Vogelbeute deutlich zunimmt. Diese Veränderung in den Nahrungsgewohnheiten wurde mittels Gewölle-Analysen (Kapitel I und III) sowie Video-Überwachung (Kapitel II) belegt.

Im zweiten Teil meiner Doktorarbeit (bisher unveröffentlichte Daten) habe ich den Ernährungs-

und Gesundheitszustand der Turmfalkennestlinge erfasst. Zu diesem Zweck wurden morphometrische Daten gemessen, um daraus einen *body-condition index* zu berechnen. Carotenoid-Messungen geben Aufschluss über die Immunkompetenz der Nestlinge, ebenso der Befall mit Ekto- und Blutparasiten sowie das Verhältnis heterophiler Blutzellen zu Lymphozyten (Kapitel IV). Im Genetiklabor wurde der Heterozygotenanteil (Kapitel V) der städtischen Population erfasst. Die Daten werden nun auch für Vaterschaftsanalysen verwendet und im Zuge einer landschaftsgenetischen Analyse ausgewertet.

Im innerstädtischen Bereich, wo Turmfalken hauptsächlich an Fassaden brüten ist, es kaum möglich adulte Brutvögel zu fangen. Um dennoch eine Blutprobe des inkubierenden Weibchens zu erhalten, modifizierten wir die non-invasive Methode zur Blutabnahme mithilfe von Raubwanzen in Kunsteiern. Die Verwendungsmöglichkeiten solcher gewonnenen Proben werden in Kapitel IV diskutiert. Zur Erfassung des Heterozygotenanteils wurden Mikrosatellitenanalysen durchgeführt. Dazu wurden genetische Marker, die ursprünglich in *F. peregrinus* und *F. naumanni* etabliert wurden, verwendet (*cross-amplification* Ergebnisse in Kapitel V).

Der letzte Teil meiner Doktorarbeit wurde in Finnland durchgeführt. Mein dortiger Betreuer stellte mir den Langzeitdatensatz eines Freilandexperimentes zur Verfügung (Kapitel VI). Seit 2003 wurden am Ende der Brutsaison zufällig ausgewählte Nistkästen gereinigt oder unberührt belassen. Bereits benutzte Nistkästen enthalten zahlreiche Gewölle, welche einen Hinweis auf eine frühere Besetzung geben ohne dass Brutvögel direkt am Nistplatz beobachtet werden müssen. Diese Information steht demnach als *public information* zur Verfügung und kann in der darauffolgenden Brutsaison von ankommenden Turmfalken für die Nistplatzwahl genutzt werden. Im Zuge der Auswertungen habe ich das Experiment um die Gegenhypothese ergänzt, nämlich dass Turmfalken einerseits benutzte Nistkästen meiden, da im Nestmaterial Ektoparasiten überwintern, welche den Bruterfolg mindern könnten. Daher evaluiere ich im letzten Kapitel die *public information* und die *ectoparasite avoidance* Hypothese gegeneinander.

Zusammenfassend leistet meine Doktorarbeit einen Beitrag zur Erklärung der hohen Brutpaardichte des Turmfalken im städtischen Raum und beleuchtet zugleich den geringeren Bruterfolg unter verschiedenen Aspekten. Dass Turmfalken von einem erhöhten Nistplatzangebot an geschlossenen Brutnischen in der Stadt angezogen werden ist auch für den Artenschutz relevant. Anhand der Ergebnisse lässt sich ableiten, dass Nistkästen nicht in Gebieten hoher Flächenversiegelung angebracht werden sollte - der Turmfalke nutzt zwar anthropogene Habitate, doch liegt seiner Nistplatzwahl eine Fehleinschätzung der Beuteverfügbarkeit zu Grunde, die eventuell sogar eine ökologische Fallensituation darstellt. Ich habe weiters einige methodische Aspekte eingeführt und genetische Daten für weitere

Forschungsvorhaben erhoben. Schließlich war ich in der Lage, in einem experimentellen Ansatz die Bedeutung von *public information* in Form von Gewöllen am Nistplatz für die Brutplatzwahl des Turmfalken zu untermauern.

1. General Introduction

1.1. Cost-benefit analysis

All behaviours are associated with costs as well as bringing benefits. An animal's decisions translate into differences in individual quality and thus prospects of survival, fecundity, or mating success and are therefore shaped by natural selection. Although natural selection should favour maximization both of reproductive outcome and of life-span, it is not possible for a living organism to achieve this combination (apart from a hypothetical 'Darwinian demon'). Life-history theory states that not all traits can be maximized simultaneously because different traits compete with one another for resources. Behavioural choices require trade-offs, compromises between different desirable but incompatible outcomes (Krebs 2009). My thesis focuses on trade-offs connected to settlement decisions.

The choice of the appropriate time and place to breed is possibly the most important decision faced by animals as it can vitally affect their productivity and survival, and as a consequence their individual fitness (Arlt and Pärt 2007; Dhondt et al. 1992; Hollander et al. 2011). Organisms are expected to choose habitats that will allow them to maximize their fitness (Fretwell and Lucas 1969) but they must divide limited resources (Levins 1968) between reproduction and other activities such as feeding. Two crucial trade-offs are central to my thesis: first, between favourable breeding sites and optimal foraging grounds; and secondly, between number and quality of offspring (Lack 1954).

My work is focused on the Eurasian kestrel (*Falco tinnunculus*, hereafter 'kestrel'). This species was chosen as a model as it is constrained by the availability of nest sites (falcons do not construct their own nests) and of prey (kestrels are highly adaptable top predators) but is flexible in its ability to exploit landscapes altered by humans. I analyse variations in breeding performance resulting from first-order effects (environmental heterogeneity, e.g. soil sealing or prey availability) and from second-order effects (interactions between conspecifics and parasite infestation).

1.2. Optimal foraging theory

The 'optimal foraging theory' (Stephens and 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 has been shown to be true when prey fluctuates in numbers between years, as the case for voles in Fen-

noscandia, which are subject to cyclic fluctuations in abundance (Kjellander and Nordström 2003, **Chapter V**) and it could also apply to the cost/benefit calculation along an urban gradient of habitat in Central Europe (**Chapter I-III**). The main prey of the kestrel is 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, 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. They may switch to prey of similar size but with poorer nutritional value if this is more readily available in inner city-districts, such as passerines. It seems likely that the cost/benefit ratio (defined by nutritional value and hunting effort) will shift along the gradient of urban habitats. I therefore hypothesize that urban kestrels will specialize in hunting birds when voles, mice and shrews are not readily available (**Chapter I-III**).

1.3. Reproduction in a changing environment

The trade-off between number and quality of offspring is reflected by the decision whether to allocate reproductive resources to fewer, high-quality offspring or to more but less viable offspring (Stearns 1992). Experimental studies of birds have improved our knowledge of the costs of reproduction. We know from experiments involving the manipulation of brood sizes in birds that reproductive effort can be negatively associated with parental condition, current reproductive success, survival and future fecundity (reviewed in Lessels 1991). Food supplementation experiments, in which levels of resources at breeding are manipulated, have provided further insights into the effects of limited resources on current reproduction (Martin 1987) and into the decisions on resource allocation made by parents (e. g. Wiehn and Korpimäki 1997; Dawson and Bortolotti 2002; Karell et al. 2004). The availability of food is the main factor influencing reproduction. Along an environmental gradient, the shift in main categories of prey would therefore be expected to have a gradual influence on breeding parameters (**Chapter I-III**). Fluctuating food conditions such as a vole cycle should create a highly variable but fairly predictable environment, so breeding performance should follow the same pattern as prey abundance (**Chapter VI**).

1.4. Bottom-up (food limitation) and top-down (predators and competitors, parasites) factors that influence individual quality

As described above, food availability is widely considered to be the major factor that determines the reproductive output and the survival of wild populations of raptors (Rutz and Bijlsma 2006). Nevertheless, there have been few previous studies of the influence of dietary shifts due to limited food resources on individual quality and fitness (but see Seward et al. 2013). To date, most studies of habitat- or diet-specific demographic parameters have relied on estimates of

individual components of quality and fitness. The results do not give a complete picture and may be misleading, as for example a low reproductive rate might be compensated by a higher rate of long-term survival. The consequences of settlement decisions can only be assessed by considering occupancy, breeding success and individual quality and fitness simultaneously (cf. (Arlt et al. 2008)). Furthermore, species respond different to heterogeneous environments, as population dynamics depend partially on foraging strategies that are able to exploit alternative food resources (Hollander et al. 2013). This ability may well assume greater significance in an urban environment.

A further topic to consider is the possibility of manipulation of the sex ratio of the offspring in response to the habitat quality. It is necessary to distinguish between the primary (full clutch) and secondary (offspring at fledging stage) sex ratios. According to the ‘sex-allocation theory’, the 1:1 sex ratio in a population is a result of frequency-dependent selection, leading to an equilibrium in which total investment in each sex is equal (Fisher 1930). When individuals of one sex are more costly to produce or to raise, as is the case in dimorphic species, sex ratios may differ from 1:1. Manipulating the sex ratio of offspring may thus represent a means for parents to adapt their reproductive efforts to the availability of resources. There is evidence that the kestrel raises more male chicks when food is scarce (Korpimäki et al. 2000), while the proportion of males in broods decreases for later clutches (Pen et al. 1999). I was interested in the possible effect of an urban gradient on the sex ratio of offspring (**Chapter I**), as Rejt et al. (2005) suggested that pairs in the centre of Warsaw produce more daughters.

There has been considerable debate on appropriate indexes to assess the fitness or quality of individuals. I considered genetic heterozygosity (**Chapter IV-V**), the presence of ectoparasites (**Chapter VI**), infestations with blood parasites (**Chapter IV**) and the heterophil/lymphocyte ratio (**Chapter IV**), which is a measurement of stress and immunocompetence (Müller et al. 2011).

1.5. Public information and conspecific attraction

Animals constantly need to acquire information about their environment and do so either by trial and error or by using social information deduced from monitoring others (Dall et al. 2005). To facilitate their settlement decision, individuals may use direct cues, such as availability of food or nest sites (the ‘direct assessment hypothesis’), or indirect cues, such as the presence of conspecifics (the ‘conspecific attraction hypothesis’, Stamps 1994) and their productivity in previous years (the ‘public information hypothesis’, Danchin et al. 1998, Doligez et al. 2003). In terms of time and energy it may be more costly to acquire personal information (Kendal et al. 2005) than social information (Valone and Templeton 2002). In fact, decisions of other individuals seem to be imitated under a wide variety of circumstances, e.g. in foraging (Valone 1989)

and in selecting habitats (Doligez et al. 2002) and nest sites (Kokko et al. 2004). The final part of my thesis considers the use of nest material, pellets and other prey remains as visible signs of the (successful) use of a nest in the previous breeding season. I thus analyse the use of public information in the settlement decision and consider whether it is advantageous to reuse a nest or to establish a new one (**Chapter VI**).

1.6. Maladaptive habitat preferences in human altered landscapes

Many species rely on environmental cues for a fast assessment of habitat quality, enabling them to reduce the time and costs of finding a suitable breeding site (e.g. Hromada et al. 2008; Kokko and Sutherland 2001; Stamps 2006). Altered environments may provide misleading cues, potentially turning them into ecological traps (Schlaepfer et al. 2002).

An ecological trap occurs when there is a mismatch between cues used in settlement decisions and the fitness consequences of these decisions during the breeding season and the post-fledging period. One such misleading cues might relate to the availability of food, which may be difficult to evaluate correctly during the stage of habitat selection and difficult to predict for the breeding season (Hollander et al. 2013; Török et al. 2004). A misevaluation of food resources might lead to a mismatch between habitat preference and habitat quality (Hollander et al. 2013; Kloskowski 2012). As a consequence, organisms may preferentially settle in low-quality habitats despite the availability of better options. I found indications that kestrels, as a city-dwelling raptor species, do indeed fall into an ecological trap when they choose to breed in historical districts of a European metropolis (**Chapter I**).

2. Aims and objectives of the study

2.1. Raptors in human altered landscapes

2.1.1. The establishment of an urban bird population

Many bird species decline once an area is urbanized (Marzluff 2001; McKinney 2006; Shochat 2004), while others increase in abundance by taking advantage of the new habitat and the altered patterns of predation and competition that attend a shift in the composition of species assemblages (Catterall 2009). As a consequence, urbanization filters bird communities (review in Shanahan et al. 2014). The success of urban species appears further to be a function of the time since the initial colonisation of urban areas (Møller et al. 2012). The urbanization of a particular species can be considered complete when the population density in urban habitats equals or exceeds the density in the ancestral rural habitat (see Moller et al. 2012; Rutz 2008).

The most highly urbanized areas are dominated by ‘urban exploiters’ (Blair 1996; Møller 2009), a small number of mainly non-native species, especially nearctic passerines (González-Oreja 2011). Urban exploiters have been defined by Shochat et al. (2006) as ‘species thriving as urban commensals to the point that they become dependent on urban resources’. Their success is thus largely related to their ability to exploit anthropogenic resources, such as garbage dumps, feeders and nest boxes (Chace and Walsh 2006). The replacement of a wide range of native species by a small number of urban exploiters has been termed ‘biotic homogenization’ (Blair 2001; McKinney 2006).

Urbanization is responsible for a high degree of habitat fragmentation, creating a patch work of resources and making it highly unlikely that any species is distributed at random. The aggregative response of individuals in patchy environments is central to population dynamics and behavioural ecology (Sutherland 1996) and may be connected to conspecific attraction (Danchin et al. 1998). I have compared the effects of urbanization and conspecific attraction on spacing behaviour in kestrels using nearest neighbour distances and information on habitat use and nest-site selection derived from a three year data set (**Chapter I**).

Due to the inability of falcons to build nest platforms, the availability of suitable nest sites seems to limit the locations where these raptors may breed (Newton 1979). There is currently no nest-box programme in the urban study system of Vienna, Austria. Kestrels breed in semi-natural nest sites on historical buildings, large numbers of which are present in the centre of the city. I hypothesize that kestrels perceive such anthropogenic cavities as favourable: the arrival times of males at such nest sites in inner-city districts are the same or slightly earlier than those of males breeding in the suburbs (see Chapter I, Table 2a).

Kestrels prey largely on voles (Village 1990) but small mammals may not be available to avian raptors in the city (Čiháková and Frynta 1996). The name house mouse (*Mus musculus*) alone suggests that this species is abundant but not available to kestrels that breed on façades and not in the basements of buildings. The same applies to nocturnal *Apodemus* species, which are abundant but hardly available to diurnal raptors. There is a clear mismatch between the abundance of prey and its availability. Hence the second hypothesis in this study predicts that the cost-benefit ratio (defined by nutritional value and hunting effort) shifts along the urban gradient (following the ‘alternative prey hypothesis’ by Lack 1954, **Chapter I-III**). In the city centre kestrels may switch to alternative prey that is both abundant and available, such as passerines or even large species, such as pigeons. In suburban areas they may prefer to fly to rural hunting grounds, where they can hunt voles (Riegert et al. 2007a; Riegert et al. 2007b).

I compared landscape composition and the specific building structure chosen by kestrels to randomly selected areas (**Chapter II**) and random buildings (**Chapter I-II**) to identify parameters of habitats and nest sites that attract kestrels to inner-city areas. To evaluate whether the

urban environment really represents a suitable habitat for reproduction, the following questions were addressed:

- (1) Which features of habitats and nest sites influence breeding success (**Chapter I-II**)?
- (2) Is the selection of the urban habitat associated with differences in annual reproductive rates (**Chapter I, II**) or a sex-bias in nestling survival (**Chapter I**)?
- (3) How does the availability of prey influence the ratio of main prey categories (**I-II**)?
- (4) Is a shift in diet detected by pellet analyses (**Chapter I, III**) and video monitoring (**Chapter II**) linked to breeding success?

2.1.2. Conspecific attraction and the value of nest box programs

The results in the urban study system are discussed with regard to the existence of an ecological trap (**Chapter I**) and I suggest possible conservation strategies (**Chapter II**). Birds (such as cavity breeders and falcons, which are within the guild of raptors) that use nests often occupy nestboxes in the year they are provided, triggering an immediate rise in breeding density (Newton 1994). Nest boxes are often considered to be the fastest and most effective way of conserving populations of cavity-dependent birds (Lindenmayer et al. 2009). However, the presence of nest boxes may attract birds to unsuitable breeding sites or induce a biased distribution of individuals in relation to habitat quality (Rodríguez et al. 2011). As kestrels are drawn to the centre of town by the high availability of nest sites, nest boxes could be employed to lure them into more suitable habitats. To identify cues from previously used breeding sites that are involved in settlement decisions, I used a data base covering eleven years of an experimental nest-box setup at a study site in Finland. I evaluated the use of pellets and prey remains as public information in settlement decisions (**Chapter VI**). It is possible that kestrels reuse nest boxes that have not been cleaned because they indicate successful broods in the previous year. To test this notion we carried out a field experiment with randomly cleaned and un-cleaned nest boxes (with pellets and other prey remains) to manipulate one indirect cue that kestrels might use for determining previous breeding success at a nest site. The prediction of the public information hypothesis is that pairs should preferentially settle in un-cleaned nest-boxes, which they interpret as being associated with an increased breeding success.

2.2. Variation in individual quality

2.2.1. Blood parasites and ectoparasites

In evolutionary biology, parasite-host interactions are of interest in relation to population regulation, to co-evolution and to animal behaviour. There is a lack of literature on bird-parasite interactions in urban areas and we have little information on ectoparasites, blood parasites and intestinal parasites. There have been limited attempts to link parasite loads to bird health, alt-

though urbanization has been shown to effect the diversity and prevalence of bird parasites (Delgado-V and French 2012). I present preliminary results on the occurrence of blood parasites in an urban study system, although the small sample size and the lack of ability to detect blood parasites in nestlings prevent the submission of a full research paper on the role of parasites in the establishment and success of urban kestrels (see **Chapter IV** for details).

Nest predation and ectoparasites are recognized as major factors in the determination of clutch-size variation in birds (O'Connor et al. 2010). Smaller clutches might be a response to high levels of parasite infestation in the nests. The levels of parasites may be higher in reused nests and blood-sucking ectoparasites that overwinter in the nest material might increase nestling mortality (Wimberger 1984). The so-called 'ectoparasite-avoidance hypothesis' might explain the observation that many raptors have a number of nest sites and use different nests in different years (see Ontiveros et al. 2008). I evaluate the prediction from the hypothesis, namely that kestrels avoid previously used nest sites when other options are available, in **Chapter VI**. The experiment essentially pits the ectoparasite avoidance hypothesis against the public information hypothesis.

2.2.2. Genetic heterozygosity

Correlations between increased genetic diversity and improvements in fitness-related traits such as reproductive success, recruitment and survival have been reported for a number of taxa. Individual heterozygosity has also been positively related to habitat quality (Seddon et al. 2004, but see Porlier et al. 2009 for a potential case of an ecological trap). The ecological differences between neighbouring urban and rural populations might be attributed to genetic diversification. Urban populations of mammals show a lower level of genetic variability and a distinctive population structure due to founder effects or to the isolation from rural populations (Wandeler et al. 2003). Newly founded populations usually consist of a few individuals (Frankham et al. 2010). The idea that kestrels in the city centre might exhibit lower levels of genetic variability has been tested on 40 nestlings in Warsaw (Rutkowski et al. 2006) but allelic diversity and heterozygosity were similar to those of rural populations. This result could be interpreted to indicate that the synurbanization process does not affect the genetic variability of birds. In contrast, a study in southern Bohemia suggested that kestrels breeding in city centres were more closely related than rural populations (Riegert et al. 2010). To investigate the genetic differentiation between birds in the city centre, in suburban areas and in rural areas, DNA was extracted from blood samples and analysed with 14 polymorphic microsatellites. Preliminary results are presented in **Chapter V** and a future project will apply a landscape genetics approach to the data set.

3. Materials and methods

3.1. Study species: Eurasian kestrel (*Falco tinnunculus*)

The Eurasian kestrel (*Falco t. tinnunculus* Linnaeus, 1758) is a widespread diurnal raptor with a Palearctic, Afrotropical and Indomalayan distribution (Ferguson-Lees and Christie 2001).

Kestrels are capable of breeding in various habitats as long as open landscapes are available for hunting (Village 1990). Depending on their breeding grounds, kestrels are resident or partially migratory; northern European populations are even long-distance migrants with birds moving into southern Europe and Africa for the winter (Village 2002). The flexibility in the choice of breeding grounds and the relatively tight time constraints for finding a suitable nest site makes the kestrel an ideal study species for investigations into the costs and benefits of settlement decisions in different landscapes altered by humans. Kestrels return to the inner-city of Vienna in February/March (Sumasgutner et al. 2014) and to breeding sites further north in Finland from March to May (Palokangas et al. 1992). 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.

Kestrels do not build a nest but scrape a shallow depression in the substrate of the chosen nest site. The most commonly used sites are the abandoned stick-nests of other bird species and ledges on cliffs or buildings (Shrubb 1993). Any structure that provides moderate protection from predators, is reasonably sheltered and can hold the eggs is a potential nest site, even attics or window boxes in high-rise flats (Charter et al. 2007a). This adaptability, together with a high degree of versatility in diet choice, probably explains why kestrels have been able to colonize such a wide variety of habitats (Village 1990).

3.2. The urban gradient

The term synurbanization (Luniak 2004), derived from the term synanthropization, denotes the adjustment of populations of wild animals to the specific conditions of an urban environment. Synurbic populations of a particular species show several significant ecological and ethological differences from populations that inhabit rural and natural areas. In **Chapter I-III** I focus on such differences for the synurbic kestrel population.

The first part of my thesis focuses on how kestrels cope with environments of varying urbanity in terms of habitat choice and foraging and breeding behaviour. Nest sites were analysed along an urban gradient from the city centre to suburban areas. The urban gradient formed a continuous variable in my statistical models and was the essential factor to which all other research parameters were related. The urban 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, housing structure, proportion of vegetation and level of anthropogenic disturbance. I calculated the urban gradient for the urban study site in Vienna in ArcGIS 10 by ESRI ©, defining it as land covered by buildings or by areas used by traffic on a land allocation map (digitized in 55 categories of land utilization between 2007 and 2010, scale 1:7,500, resolution 15 cm), in a circle of radius 500 m around the nest sites or random points, *sensu* (Zuckerberg et al. 2011). Areas with < 1% of unsealed 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.

Nests were distributed between percentages of sealed soil of 18% (most suburban) and 89% (most urban). By extending the search up to >1% soil sealing ensured that nearest neighbour distances were accurate.



Fig. 1. Urban gradient in three urban zones: city centre with 81%-89% soil sealing (red), mixed zone with 51-80% soil sealing (blue) and suburban area with 18-50% soil sealing (green) in the city of Vienna, Austria.

Depending on the sample size it was necessary to pool the data for some analysis. I defined three urban zones to ensure a) comparability with other studies (e.g. Kübler et al. 2005); b) equal sample size in each zone; and (c) that the historical building structure could be taken into account.

In **Chapter I** I focus on the urban gradient and present mean values of breeding parameters and diet data (details in **Chapter III**) pooled for three zones to underline the differences: city centre with 81%-89% soil sealing, mixed zone with 51-80% soil sealing and suburban area with 18-50% soil sealing (Fig. 1). In **Chapter II** I take the historical building structure into account. Doing so necessitates a change in the boundaries to the following: city centre (the old town in 1775, see Berger and Ehrendorfer 2011, recent impervious surfaces of > 75%), the mixed zone (parts of the old town in 1775 located along the green riverside and surrounding former cultivated landscapes, recent impervious surfaces of 45-75%) and the suburban area (recent outskirts of Vienna with impervious surfaces of <45%). Each nest site was assigned to one of these

zones (Chapter II, Supplementary Material 1).

3.3. Experimental nest-box setup

For the third part of my thesis, the study area was situated in the Kauhava and Lapua region, western Finland (62°59'-63°10'N, 22°50'- 23°20'E). The study sites are adjacent areas consisting of two contrasting habitats. The first is a homogeneous open habitat (>70% agricultural fields) covering an area of 170 km², consisting of the so-called 'Alajoki field' along the river Lapuanjoki between Kauhava and Lapua. The area is composed of a level, uniform agricultural landscape broken by small islands of trees, bushes and woods and by large ditches. The second area is a heterogeneous habitat (25-30% agricultural fields) covering an area of 260 km² that consists of a collection of small fields between Kauhava and Lappajärvi (Fig. 2).



Fig. 2: Study area in south Ostrobothnia region in western Finland.

From autumn 2002 to the breeding season of 2013 between 35 and 119 kestrel nest boxes each year were included in an experimental setup in the study area (mean=78.6, *SD*=31.4). Each year we randomly assigned each nest box to one of two groups: treatment (pellets and prey remains were removed in autumn and hay and straw as nest material were renewed, i.e. a clean nest box, *n*=366) and control (pellets, prey remains and old nest material were left inside, i.e. an uncleaned nest-box, *n*=498). The study area is characterized by a high annual turnover of breeding kestrels (on average 90% of females and 68% of males are new, pooled data from 1985 to 2010). The 'divorce rate' is also very high, with 82% of female kestrel parents that return to breed in the study area mating with a different male the following year (pooled data from 1985 to 2010 for females whose previous partner was documented to be still alive, see Vasko et al. 2011 for details). For these reasons, it is highly unlikely that kestrels directly observe previous breeding success at the site, so the use of pellets and other prey remains as indirect cues of previous breeding success may be favoured. The study population in Finland was extremely useful for testing the predictions of the public information hypothesis and the ectoparasite avoidance hypothesis (Fig. 3, **Chapter VI**).



Fig. 3: Experimental nest-box setup with randomly cleaned and un-cleaned sites (pellets and other prey remains left).

3.4. The predator-prey study system: Eurasian kestrels and availability of prey

3.4.1. Small mammal survey

In the urban study area of Vienna small rodents were trapped using Rödl-type live traps (Janova et al. 2010). The traps were 24 cm long, 6 cm wide and 6 cm high. Depending on the specific habitat type at a site, 10-20 traps were placed at 10 m intervals. Distinctive structures such as ditches, slopes and trees were preferentially used, as they represent good sites for trapping small mammals (Spitzenberger and Steiner 1967). We used the 'minimum number alive' method (Krebs 1996) to calculate rodent densities (**Chapter I**).



Fig. 4: Aerial image of Vienna city centre (Z, Photo: TU Wien). 1 = Volksgarten, 2 = Maria-Theresien Park, 3 = Burggarten, 4 = Stadtpark, 5 = Schlossgarten Belvedere, 17 = Augarten, 18 = Donauinsel.

Each site was sampled for 48 hours, with the traps checked twice a day, once in the morning and once in the evening. During 2676 trapping units, 129 adult *Apodemus* individuals were caught, including 49 *A. flavicollis*, 55 *A. sylvaticus* and 9 *A. uralensis*. The study lasted from May to September 2010. The order of trapping in parks was determined randomly to avoid a possible bias. Traps were baited with high-energy peanut butter (78% fat, 9% carbohydrates und 13% protein). In the urban study area, 23 parks were randomly selected (Fig. 4, size between 1.1 and 600ha, between 0.6 and 9 km from the city centre).

Vole trapping has been carried out at the Finnish study site from 1985 to 2010 to quantify the abundance of vole within and between years. Snap-traps were laid in early May and mid-September in sample plots in the four main types of habitat: cultivated fields, abandoned fields, spruce forest and pine forest. Between 50 and 100 Finnish metal mouse snap-traps were set at 10 m intervals in vole runways on each plot. They were baited with mixed-grain bread and were checked daily for four days. The area of a sample plot ranged from 0.5 to 1.0 ha. We pooled the results from four nights of trapping and standardized them to the number of animals caught per 100 trap nights in each habitat type (see Korpimäki and Wiehn 1998 for details). Abundance indexes of voles of the genera *Microtus* (the field vole *M. agrestis* and the sibling species *M. rosaliae*) and *Myodes* (the bank vole *M. glareolus*) were pooled for each type of habitat as these species are the main prey of kestrels in Finland (Korpimäki 1985). The results are presented as vole index in spring and vole index in (previous) autumn (previous to the breeding season).

3.4.2. Avian prey

In 2010 (**Chapter I**) and 2011 (data from both years used in **Chapter II**) a field survey determined the abundance of potential avian prey for kestrels breeding in urban areas of Vienna. A team of 31 assistants monitored 33 transects in the course of a breeding bird survey to assess the status of the bird population. Transects were sampled twice per year at the beginning of the breeding season: once in spring, calendar week 17-18 in April, which coincides with the nestling period of kestrels; and once in summer, calendar week 22-23 in June. We used the standard method of point-counts with birds identified to species (Südbeck et al. 2005). Each transect consisted of 12 to 20 points (distributed along 3.6 to 6 km) evenly spaced at 300-500 intervals. We ensured that the points were distributed across the following habitat types to characterize the urban study area: city centre (C), green backyard (B) and park (P), garden (G) and forest (F). I estimated total species richness per habitat type using non-parametric species richness estimators in Estimate S 8.0 (Colwell, 2006): Sobs (number of species expected in the pooled samples, given the empirical data) and Chao1 (abundance-based coverage estimator, chosen according to Brose and Martinez (2004)). The resulting estimates of total species richness per habitat type enabled me to calculate the completeness of our species inventories.

During the bird census (pooled data from 2010 and 2011), we recorded 89 bird species ($n = 1,511$ point count units, 75 species in 2010 and 80 species in 2011). The estimator curve (Chao 1) indicates that the expected total species richness represents a reliable estimate for all habitat types (Fig. 5). Both the species richness and the abundance-based coverage estimator showed a decline of species richness from forested areas to the city centre: F ($n = 184$ point count units, 64 species observed vs. 88 species expected) > P ($n = 267$, 61 obs. vs. 69 exp.) > G ($n = 427$, 65

obs. vs. 67 exp.) > B ($n = 259$, 43 obs. vs. 58 exp.) > C ($n = 374$, 34 obs. vs. 57 exp.).

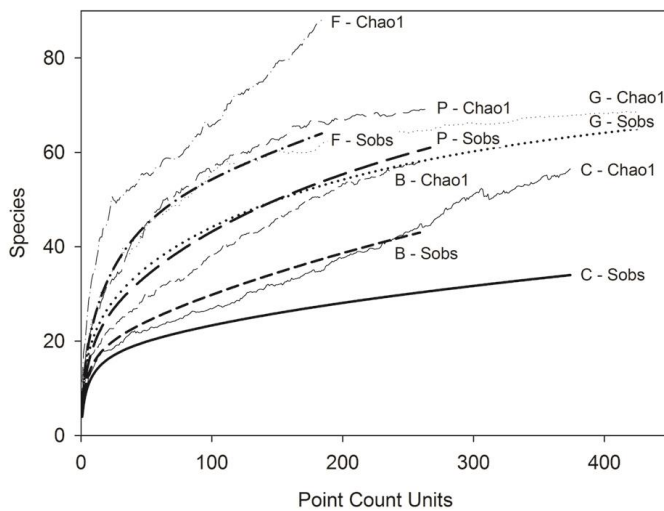


Fig. 5: Species accumulation curves (Sobs, Mao Tao function) and abundance-based species estimator curve (Chao 1) for bird assemblages in the different urban habitat types in Vienna: city centre (C), backyard (B), park (P), garden (G) and forest (F).

3.5. The host-parasite study system: Eurasian kestrels and their parasites

The most abundant ectoparasite of *F. tinnunculus* is the blood-sucking fly *Carnus haemapterus*. The level of infestation increases from birth to 16 days of age (Fig. 6) but it subsequently declines and at fledging nestlings are virtually free of the parasite. Adult parasites are hematophagous and can largely be found on bald areas, usually under the wings, while larvae are sapro-trophic and thought to live in the nesting material until they pupate and move to a host (Grimaldi 1997). Kestrels living in nest boxes are more likely to be attacked by ectoparasites than pairs in other types of nests (Fargallo et al. 2001). When ectoparasites are still rare in the few days after hatching, *C. haemapterus* are mainly located on the nestlings that hatch first but as nestlings grow the number of parasites increases and the nestlings that hatch last become the most highly infested (Roulin et al. 2003). Susceptibility to ectoparasites was assessed by the number of ectoparasitic flies *C. haemapterus* and *Crataerina melbae* and European castor-bean ticks *Ixodes ricinus* on the nestling body (the latter is found only in the urban study system, data not shown).

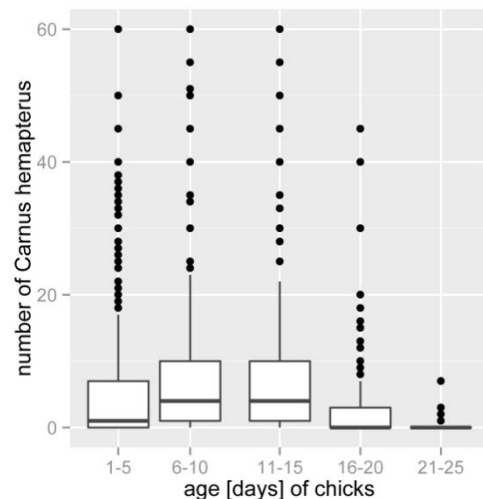


Fig 6. Number of *Carnus haemapterus* on the host related to the age of nestlings in the Finnish kestrel study population. X-axis – age of kestrel chicks [days] in 5 categories, Y-axis – average number of *C. haemapterus* individuals per nestling ($n = 256$ nest boxes in 2011 and 2012).

Kestrels also host a number of other blood parasites, including haemosporidians, zooflagellates and nematodes. These are cosmopolitan and have been reported from more than 2/3 of the avian species examined (Atkinson and van Riper III 1991). The haemosporidians commonly found in avian blood belong to the genera *Leucocytozoon* and the avian malarial parasites *Haemoproteus* and *Plasmodium*. The parasites infect blood cells and use them as hosts to produce gametes. Zooflagellates of the genus *Trypanosoma* and nematodes (microfilarial worms) are common intercellular parasites in avian blood (Atkinson and van Riper III 1991). An infected blood cell in the host cannot function properly as it produces gametes for the parasite. In the urban study population, I found *Haemoproteus* only in adult kestrels, not in chicks (**Chapter IV**, Fig. 7); in the Finnish population I could detect *Haemoproteus*, *Leucocytozoon* and *Trypanosoma*. The data have not yet been published.

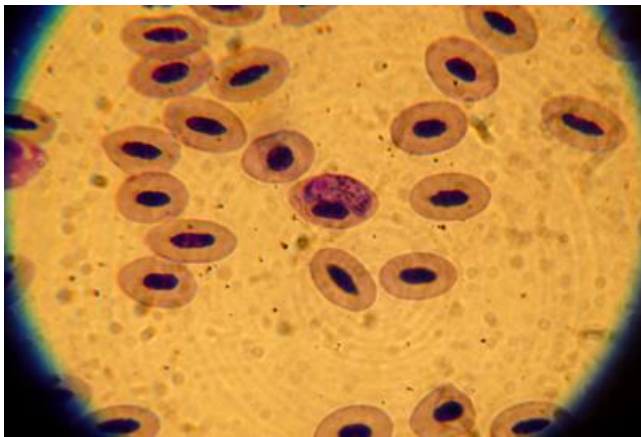


Fig. 7: *Haemoproteus* sp. in avian erythrocytes.

Part 1

Chapter I: Sumasgutner P, Nemeth E, Tebb G., Krenn HW, Gamauf A (*accepted*) 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*.



Photo: Harald Mannsberger

Hard times in the city - attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey

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Abstract

Introduction: Urbanization is a global phenomenon that is encroaching on natural habitats and decreasing biodiversity, although it is creating new habitats for some species. The Eurasian kestrel (*Falco tinnunculus*) is frequently associated with urbanized landscapes but it is unclear what lies behind the high densities of kestrels in the urban environment.

Results: Occupied nest sites in the city of Vienna, Austria were investigated along a gradient of urbanization (percentage of land covered by buildings or used by traffic). Field surveys determined the abundance of potential prey (birds and rodents) and the results were compared to the birds' diets. A number of breeding parameters were recorded over the course of three years. The majority of kestrels breed in semi-natural cavities in historic buildings. Nearest neighbour distances (NND) were smallest and reproductive success lowest in the city centre. Abundance of potential prey was not found to relate to the degree of urbanization but there was a significant shift in the birds' diets from a heavy reliance on rodents in the outskirts of the city to feeding

more on small birds in the centre. The use of urban habitats was associated with higher nest failure, partly associated with predation and nest desertion, and with significantly lower hatching rates and smaller fledged broods.

Conclusions: High breeding densities in urban habitats do not necessarily correlate with high habitat quality. The high density of kestrel nests in the city centre is probably due to the ready availability of breeding cavities. Highly urbanized areas in Vienna are associated with unexpected costs for the city dwelling-raptor, in terms both of prey availability and of reproductive success. The kestrel appears to be exploiting the urban environment but given the poor reproductive performance of urban kestrels it is likely that the species is falling into an ecological trap.

Keywords: diet choice, ecological trap, *Falco tinnunculus*, historical building structure, nest site choice, nest survival, prey availability, urban exploiter, urban gradient

1. Introduction

Rapidly increasing urbanization is a global phenomenon that affects not only humans but also animals and plants (Ramalho and Hobbs 2012). While native biodiversity often declines (Marzluff 2001), urbanization promotes the biotic homogenization of species assemblages (Lososová et al. 2012; McKinney 2006; Rensburg et al. 2009). Because of the loss of natural habitat, urbanization generally leads to a complete restructuring of vegetation and species composition and has thus become a major concern in conservation biology (McDonald et al. 2008; Miller and Hobbs 2002).

The urban environment can induce dramatic changes in animal behaviour, physiology and life-history (Dominoni et al. 2013; Nemeth and Brumm 2009; Slabbekoorn and Ripmeester 2008; Zhou and Chu 2012). Within species, studies on passerines have shown that urban individuals have smaller clutches that are generally laid earlier and that their nestlings are lighter than those of their rural conspecifics (Chamberlain et al. 2009). Ultimately, species able to adapt to the challenges posed by increasing urbanization will persist and may even increase, while those that cannot will decline or disappear. Urbanization thus filters bird communities (review in Shanahan et al. 2014).

The success of urban species appears to be a function of the time since they initially colonized urban areas (Møller et al. 2012). The most highly urbanized areas are dominated by 'urban exploiters' (Blair 1996; Møller 2009), a small number of mainly non-native species, especially nearctic passerines (González-Oreja 2011), whose success in urban areas is largely related to their ability to exploit human resources such as garbage dumps, feeders and nest boxes (Chace and Walsh 2006). Many other species are also found in the centres of large cities, although it is often hard to determine whether they are benefitting or suffering from the urban environment. It is conceivable that the decision to breed in highly urbanized areas might be based on a mistaken assessment of the quality of the environment, with individuals in urban centres suffering from a lower availability of food and lower breeding success. In such cases, the species is said to have fallen into an 'ecological trap' (Schlaepfer et al. 2002).

The Eurasian kestrel (*Falco tinnunculus* Linnaeus, 1758) is clearly affected by urbanization. It was first recorded breeding in urban environments in the latter half of the 19th century (Cramp and Tomlins 1966) and is now commonly associated with urbanized landscapes (Kostrzewa and Kostrzewa 1993). A number of studies have been performed on the diet and breeding success of urban kestrels (e.g. Darolová 1992; Piattella et al. 1999; Rejt 2001; Romanowski 1996; Salvati et al. 1999; Sommani 1986) but it is difficult to draw general conclusions from them, as each metropolis provides a unique habitat, differing from others in terms of size (Garaffa et al. 2009), building structure (Sorace and Gustin 2009) and composition of vegetation (Lerman et al. 2012; Pellissier et al. 2012). Despite the previous work, it is still unclear whether the kestrel is a true

urban exploiter or whether instead the urban environment represents an ecological trap for the species. The issue can best be addressed by analysing the breeding success of members of an urban population that is sufficiently large to permit the comparison between 'city-dwellers' and birds living in the suburbs.

The urban study area in Vienna (243 km²), Austria has the highest documented density of Eurasian kestrels in a non-colonial urban breeding population (Sumasgutner et al. 2013; Wichmann et al. 2009, c.f. Darolová 1992; Piattella et al. 1999; Rejt 2001; Romanowski 1996; Salvati et al. 1999; Sommani 1986) and is ideally suited to a study of this kind. We compared the species' biology along an urban gradient, defined by the density of buildings and areas used by traffic (Kübler et al. 2005). We considered (1) whether the breeding density of kestrels in urbanized landscapes results mainly from the availability of nest sites, based on the historical building structure and asked (2) whether the use of the urban habitat is associated with differences in annual reproductive rates or (3) a sex bias in nestling survival. We also (4) analysed causes of nest failure and tested whether (5) there is a link between breeding density, reproductive success and availability of prey. Because of the data structure and the relatively small sample size, we pooled the nests investigated more closely into three defined urban zones, using the different zones as discrete explanatory variables (6) to examine the main categories of prey in the kestrels' diet and (7) to relate the diet to the availability of prey.

2. Results

2.1. Nest site choice and nest site availability

The kestrel monitoring in 2010 found a total of 251 occupied nests, while in 2011 297 nests and in 2012 215 nests were found (Fig 1). The figures translate to a breeding density of 89-122 breeding pairs per 100 km² in urbanized areas of Vienna. Kestrels predominantly breed in building cavities (69%, based on nests occupied in 2010), where they largely use roof openings (41%). Abandoned crow nests in trees are less frequently used (18% of broods). In rare cases, nest boxes (6%; 33 nest boxes were offered in the city) or window boxes (4%) are used.

The nearest neighbour distance (NND) decreases significantly with an increasing percentage of sealed soil (measured in a circle of radius $r=500$ m around the nest site, Pearson Correlation, $N_{(2010)}=251$, $r=0.47$, $P<0.001$, Figs 1 and 2). An analysis of microhabitat variables showed that the structure of buildings with nest sites differed significantly from those of buildings selected at random (Table 1). Unobstructed roof openings and the availability of green courtyards are more frequent at nest sites than at randomly chosen buildings. Accessible roof openings in buildings chosen at random are only found in the historical city centre with a soil sealing factor of more than 52%.

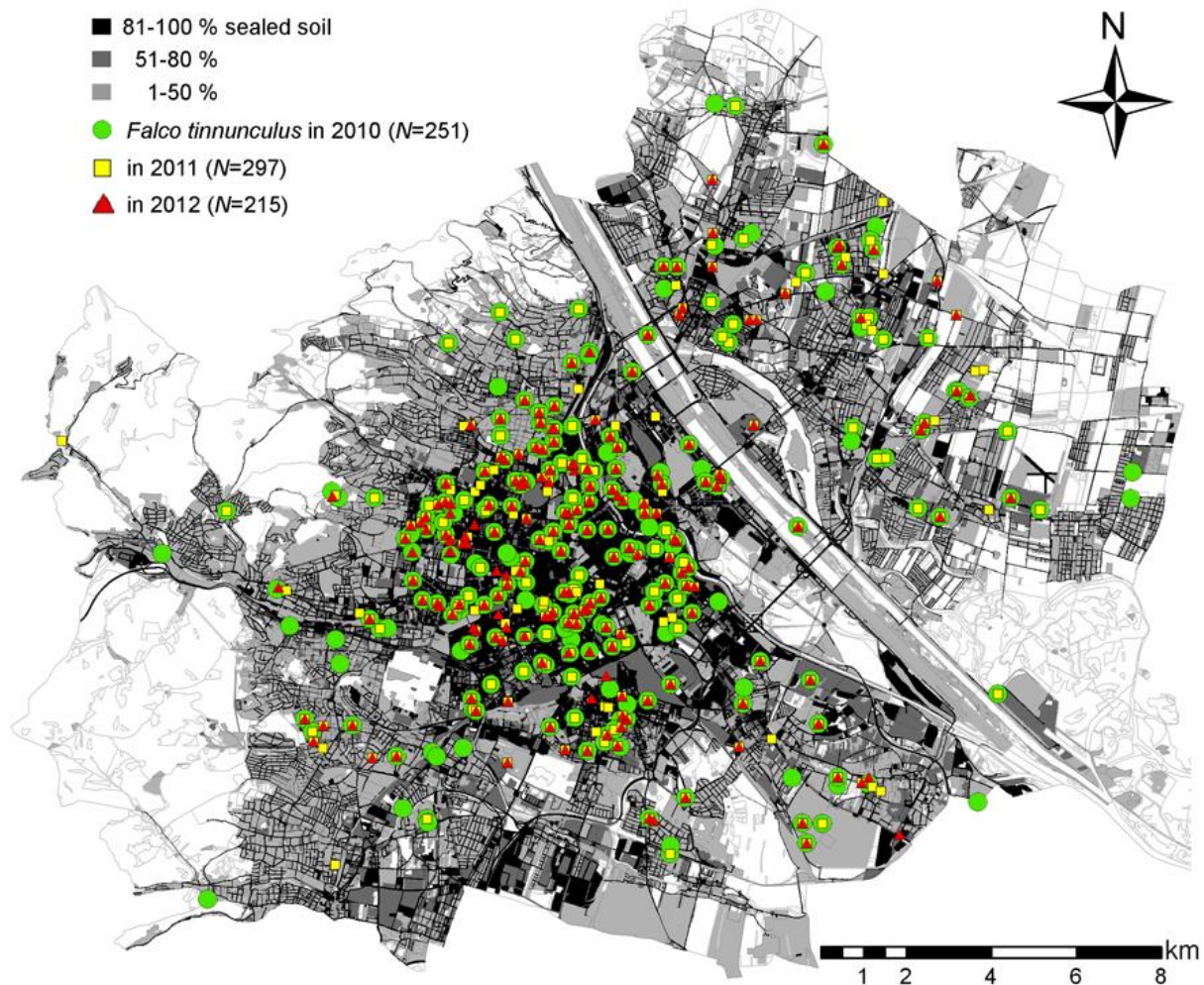


Figure 1: Urban study area (243 km²) in Vienna, Austria. The urban gradient, displayed from black to grey (white - unsealed soil outside the study area), and occupied nest sites of *Falco tinnunculus* during the study period (2010 – 2012).

Table 1: Habitat differences between buildings chosen at random (N=240) and nest sites (N=195) on buildings shown with a GLM with binomial error structure (random point = 0, nest site = 1) and a logit link function.

Variable	Estimate	SE	T-value	P-value	Sign.
Intercept	-3.11	0.70	-4.46	< 0.0001	***
Roof-openings [open = 1, closed = 0]	4.12	0.50	8.29	< 0.0001	***
Façade [smooth = 0, not smooth = 1]	-0.46	0.26	-1.79	0.07	•
Nest height/Height of the attic [m]	0.29	0.10	3.22	0.002	**
Green courtyard [yes = 1, no = 0]	0.88	0.27	3.33	<0.001	***

Significance codes: '***' 0.001, '**' 0.01, '•' <0.1.

Unlike their conspecifics in some other European cities (e.g. Darolová 1992; Riegert and Fuchs 2011; Romanowski 1996), kestrels temporarily leave Vienna during winter and return in spring. The dates when kestrels arrived at their nest sites differed only slightly along the urban

gradient (Table 2a, $P=0.06$). In 2010, kestrels arrived at breeding sites in the city centre on average 3 days (± 3.7 SD) earlier than at sites in suburban areas and in 2011 the difference was 7 days (± 5.0 SD). Males usually occupied nest sites before females but the arrival dates of the two sexes overlapped.

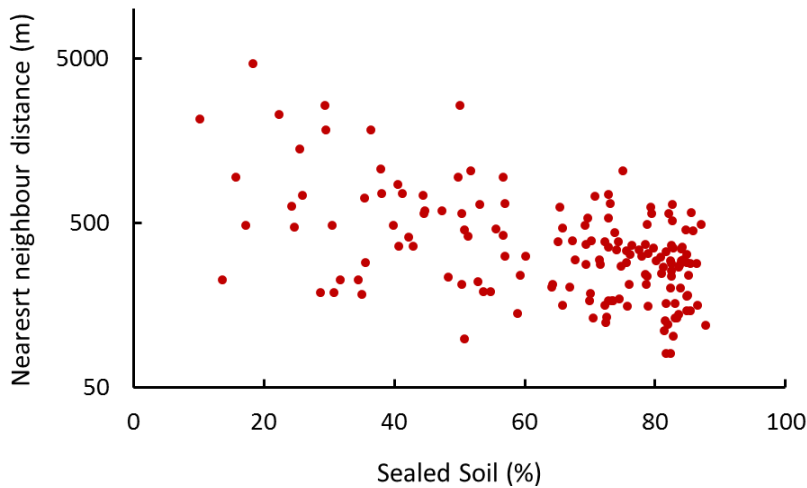


Figure 2: Sealed soil (%) and nearest neighbour distance (NND) between occupied nest sites of *Falco tinnunculus* in the study area in Vienna, Austria.

2.2. Breeding success and nestling survival along the urban gradient

There was no obvious effect of the urban gradient on the laying date (Table 2a). The ratio of eggs hatched and the sizes of fledged broods depended upon the percentage of sealed soil and the laying date, both of which significantly decreased towards the city centre and for later broods (Table 2b). Differences in urbanization and laying date were sufficient to account for 32% of the variance (R^2 for GLMM) in breeding success (number of fledglings). The clutch size and the fledging rate were significantly influenced by the laying date, with fewer eggs and fewer fledged hatchlings in later nests (Table 2b). The mean values and SD for the breeding data are given in supplementary material 2.

We found a primary sex ratio of 47% female and 53% male offspring (variation from hypothesized 1:1 ratio, $N=71$ broods, exact binomial test 2011: $P=0.82$; 2012: $P=0.22$), whereas the sex ratio at fledging was 54% female and 46% male ($N=91$ broods, $0.23 < P < 0.33$). Female offspring have a slightly higher rate of survival; of the chicks lost as nestlings ($N=54$ individuals), 31% were females and 69% were males ($\chi^2=3.84$, $P=0.05$).

Table 2a: Dependence of breeding time (2010-2012) on the urban gradient (measured as percentage of sealed soil in $r=500$ m around the nest site) and nearest neighbour distance (NND) as fixed effect in a generalized linear mixed model (GLMM). The nest site ID and the study year were included as random factors. The error family was chosen according to the type of response variable as Gaussian family and identity link function. Explanatory deviance (in %) is given for each fixed effect.

(a) Breeding time	Estimate	SE	T -value	$Pr(> t)$	expl.dev.(%)	Sign.
Arrival date [†] ($N=333$)						
Sealed soil	-12.36	6.47	-1.91	0.0568	54.74	•
NND [†]	-2.49	2.90	-0.86	0.3920	13.85	NS
(Intercept)	272.53	14.33	19.01	<0.0001		***
Laying date [†] ($N=157$)						
Sealed soil	7.95	6.79	1.17	0.2440	40.68	NS
(Intercept)	28.53	4.86	5.85	<0.0001		***

Note: [†] data presented as residuals with the study year, [†] log transformed
Significance codes: '***' 0.001, '•' <0.1, 'NS' not significant.

Table 2b: Dependence of breeding parameters (2010-2012, $N=157$) on the urban gradient (measured as percentage of sealed soil in $r=500$ m around the nest site) as fixed effect in a generalized linear mixed model (GLMM). The nest site ID and the study year were included as random factors. The error family was chosen according to the type of response variable.

(b) Breeding parameter	Estimate	SE	Z-value	$Pr(> z)$	R^2 for GLMM	Sign.
Clutch size ($N=138$)					4.5	
Laying date [†]	-0.01	0.00	-2.48	0.0132		*
(Intercept)	1.54	0.04	38.80	<0.0001		***
Hatching rate					15.44	
Laying date [†]	-0.04	0.01	-2.94	0.0033		**
Sealed soil	-2.40	1.07	-2.23	0.0255		*
(Intercept)	2.54	0.78	3.24	0.0012		**
Fledging rate					16.04	
Laying date [†]	-0.04	0.02	-2.06	0.0399		*
Sealed soil	-2.13	1.25	-1.71	0.0882		•
(Intercept)	2.60	0.99	2.62	0.0087		**
Fledged brood size					32.31	
Laying date [†]	-0.02	0.00	-4.54	<0.0001		***
Sealed soil	-0.85	0.34	-2.48	0.0131		*
(Intercept)	1.26	0.25	5.04	<0.0001		***

Note: [†] data presented as residuals with the study year
Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '•' <0.1.

2.3. Causes of nest failure

The initial fixed-effects model of nest survival included laying date and the percentage of sealed soil (Table 3). The best model shows daily survival rates decreasing with percentage of sealed soil from the suburbs towards the city centre and with later laying dates. As there was only a slight difference from the model that includes the age of the nestlings when the nest was found, we are confident that the results are not biased by when breeding was confirmed (during incu-

bation or during the nestling phase). We tested for the influence of NNDs on nest failure, as reproductive performance is expected to decline with increasing population density, but the resulting model did not meet the criteria for good candidate models. To test tolerance against a potential anthropogenic stressor, we incorporated areas used by traffic in one model but in contrast to the observations on American kestrels (*Falco sparverius* (Strasser and Heath 2013)) we found no correlation.

A total of 33% of nests failed, with no statistically significant differences between years (Kruskal-Wallis $\chi^2_{(2, 157)}=2.06$, $P=0.36$). 83% of nest failures occurred during incubation, with 27% of failures connected to predation as confirmed by direct observation (Table 4) and 29% due to nest desertion. Hooded crows (*Corvus cornix*) and Carrion crows (*Corvus corone*) are both common in Vienna but we found no significant difference in the abundance of these potential nest predators along the urban gradient ($Z=0.76$, $P=0.45$).

Table 3: Summary of model-selection according to Mark (Laake et al. 2013) for fixed-effects models of daily survival rate for kestrel nests ($N=157$). K is the number of parameters in the model and ω_i the model weight.

Model	K	AIC _c	Δ AIC _c	ω_i
Laying date [‡] + Sealed soil (%)	3	271.42	0.00	0.5659
Laying date [‡] + Sealed soil (%) + Age found	4	272.19	0.77	0.3852
Laying date [‡]	2	276.61	5.19	0.0422
Distance (m) [†] from closest open green space (≥ 1 ha) + Sealed soil (%)	3	282.05	10.62	0.0028
Presence/absence of green courtyard + Sealed soil (%)	3	282.88	11.45	0.0018
Sealed soil (%)	2	283.86	12.44	0.0011
Age found + Sealed soil (%)	3	284.89	13.47	0.0007
Nearest neighbour distance (m) [†]	2	288.30	16.88	0.0001
Age found	2	290.46	19.04	0
Intercept-only model (constant daily survival rate)	1	290.49	19.07	0
Time Trend	2	290.89	19.47	0
Traffic area (m ² , in $r=100$ m around the nest site) [†]	2	291.27	19.85	0

Note: '‡' data presented as residuals with the study year, '†' log transformed

Table 4: Number of nest attempts, reproductive outcome and cause of complete nest failure for *Falco tinnunculus* in Vienna, Austria 2010-2012.

Year and nest attempts	Reproductive outcome		Time of nest failure		Cause of nest failure		
	Success (%)	Failure (%)	Egg stage	Nestling stage	Abandoned	Predation [#]	Other
2010: 36	21 (58%)	15 (42%)	11	4	5	4	6
2011: 52	36 (69%)	16 (31%)	14	2	4	6	6
2012: 69	48 (70%)	21 (30%)	18	3	6	4	11
Total: 157	105 (67%)	52 (33%)	43	9	15	14	23

Note: [#] based on confirmed predation. If the predation event was not directly observed and the predator not identified, nest failure is assigned to other.

2.4. Availability of prey

No significant relationship was found between abundance of prey and breeding success. Neither the number of prey-sized birds nor the abundance of rodents was able to predict the occurrence of successful breeders (GLM with proportion of successful nests per transect as dependent variable with binomial error distribution and logit link function (Crawley 2007) and both average numbers of birds and rodents as two predictors in the model, $N=25$ transects, P for all predictors was not significant; birds: $Z=1.13$, $P=0.25$; rodents: $Z=0.42$, $P=0.42$).

The abundance of prey-sized species of bird varies with location along the urban gradient. No difference was found for thrush-sized birds (GLM with urban zone as predictor variable $Z=0.91$, $P=0.36$) but sparrow-sized birds were more abundant in suburban areas ($Z=11.08$, $P<0.001$) and pigeons – which our pellet analysis confirmed were included in kestrels' diet – were more abundant in the city centre ($Z=3.49$, $P<0.001$).

The rodent survey included 2,676 trapping events ($N=129$ individuals) and caught almost exclusively field mice of the genus *Apodemus* (98.4% of three species, *A. sylvaticus*, *A. flavicollis* and *A. uralensis*), with very small numbers of house mice *Mus musculus*, brown rats *Rattus norvegicus* and bank voles *Clethrionomys glareolus* recorded. In view of the relatively minor importance of field mice in the diet of urban kestrels (see below) and of the small sample size, an analysis of the trapping data by urban zone was not undertaken. Of the species trapped in the survey, only the bank vole is active by day (Jenrich et al. 2010), so the results indicate that diurnal rodents are hardly available in the city. The situation is in stark contrast to the surrounding areas, where diurnal voles (especially *Microtus arvalis*) are common (Mitter et al. 2013; Spitzenberger 2001).

2.5. Diet choice in three urban zones

Pellet analysis showed no difference in the proportions of the main categories of prey between years (Kruskal-Wallis χ^2 -test: 0.22, $P<0.62$). There were differences between urban zones: pellets in the city centre ($N=18$ nest sites) consisted of 48.5% (by biomass, for details of calculation see Materials and Methods) mammals, 39% birds, 3.5% reptiles and 9% insects, while pellets found in the mixed zone ($N=10$ nest sites) consisted of 56.6% mammals, 29.8% birds, 1.5% insects and 12.1% reptiles. The pellets found in suburban areas ($N=9$ nest sites) showed 79.6% mammals, 12.2% birds, 4% insects and 4.2% reptiles. We could not identify all pellet contents to the species level but 70.4% of small mammals that could be identified were *Microtus arvalis* voles (sub-sample size: $N=152$ individuals). Other mammal species identified were 13.0% field mice (*Apodemus* spp.) and 8.3% shrews (Soricidae).

The ratio of pairs that preyed mainly on mammals as opposed to on birds (based on the estimated biomass per nest site) differed significantly between urban zones (mammals: Kruskal-Wallis $\chi^2_{22}=7.54$, $P=0.02$ and birds: $\chi^2_{22}=7.24$, $P=0.03$), as did Levin's index for breadth of diet, which was highest in the city centre (Kruskal-Wallis $\chi^2_{22}=8.34$, $P=0.02$; Levin's index in the city

centre: 4.02, mixed zone: 3.10 and suburban area: 1.44). Reptiles were preyed upon more often in the mixed zone (Kruskal-Wallis $\chi^2_2=5.67$, $P=0.06$), while insects were taken at approximately equal amounts in all urban zones (Kruskal-Wallis $\chi^2_2=0.61$, $P=0.74$).

3. Discussion

3.1. Choice and availability of nest site

Nearest neighbour distances (NND) decreased with increasing percentage of sealed soil (Fig 2) but pairs in the city centre had lower reproductive success, measured in terms of hatching rates and sizes of fledged broods, than pairs in suburban areas. As falcons do not construct nests themselves, their breeding locations are limited by the availability of potential nest sites (Newton 1979; Village 1983). The correlation between the number of nest sites and the number of roof openings (Table 1) supports the notion that more kestrels breed in the city centre due to the greater availability of building cavities. This can be attributed to the structural element of roof openings, which are limited to historical buildings in the city center.

Many species rely on environmental cues for a rapid assessment of habitat quality, thereby reducing the time and cost of finding a suitable breeding site (e.g. Hromada et al. 2008; Kokko and Sutherland 2001; Stamps 2006). In environments that have been altered, the use of cues that were formerly reliable might lead to reduced reproduction, turning these environments into ecological traps (Schlaepfer et al. 2002). Most ecological traps have an anthropogenic origin (Robertson and Hutto 2006) and migratory species might be more likely to fall into ecological traps created by urban landscapes (Battin 2004); compared to residents, migratory birds have more stringent time constraints in assessing the quality of breeding sites (Fuller 2012; Gamauf et al. 2013; Hromada et al. 2008). Early arriving individuals usually have preferential access to the best sites and partners, while later arrivals must settle in territories of progressively lower quality (Chalfoun and Schmidt 2012; Sergio et al. 2007). For territorial birds such as the kestrel this should result in a sort of ideal-despotic distribution (Fretwell 1972) where males first occupy the best sites, with poorer sites occupied successively later. We would expect the territories occupied first to show the highest breeding success but our study revealed the opposite to be the case. Kestrels breeding in the centre of Vienna tended to arrive before their suburban conspecifics (Table 2a), suggesting that inner-city sites are assessed as being of at least equal quality. However, there were no differences in laying dates along the urban gradient and breeding performance (Table 2b) was worse in inner-city districts than in the outskirts. Thus, the first returning kestrels do not select the best breeding sites. Breeding in highly urbanized areas was associated with higher rates of nest failure. Our models of nest survival showed that the percentage of sealed soil and the laying date are the main variables connected to nest failure (Table

3). A close proximity to large open green spaces (≥ 1 ha) and the presence of green courtyards also increased nest survival.

If highly urbanized areas are not associated with a breeding advantage, why are they occupied ahead of more productive sites at the edge of the city? It is possible that there are simply too few breeding cavities in the outskirts of the city. We found nest site cavities exclusively in the centre and conclude that closed breeding cavities are chosen because of their attractiveness and not because of the limited numbers of other potential types of nest, such as crow nests and window boxes. Attributes of breeding cavities such as limited accessibility to predators, protection from rain and sun and a low probability of collapse have been associated with higher breeding success (Charter et al. 2007; López et al. 2010). Our study appears to show the opposite, with the selection of breeding cavities in the city centre associated with a lower breeding success.

3.2. Nest failure, breeding success and sex-biased nestling survival

Most nest failures occurred during incubation of the eggs and were connected to nest desertion or predation (Table 4). Our results do not indicate a lower rate of nest predation for urban-breeding birds, as has been documented in other studies (Stracey 2011; Tella et al. 1996) but see (Evans et al. 2009) reporting higher nest predation by corvids in urban areas). Abandonment occurred during the egg stage (once after hatching) and might have related to territorial disputes or to higher ectoparasite burdens in breeding cavities.

In common with many other raptors, the kestrel shows a size dimorphism, with females larger than males (Village 1990). When individuals of one sex are more costly than the other to produce, sex ratios may differ from 1:1 (Clutton-Brock 1986). A higher mortality of the more expensive sex results in an excess of the cheaper sex at fledging and several species of raptor are known to manipulate the sex ratio of their offspring in response to a range of factors (e.g. Anderson et al. 1997; Ingraldi 2005; Wu et al. 2010), including variation in the availability of resources (Millon and Bretagnolle 2005; Rutz 2012). Kestrels have been reported to switch the sex-bias from male-dominated in early nests to female-dominated in later nests (Dijkstra et al. 1990). We found that the smaller males and the last chicks to hatch were most likely to die as nestlings. The results are consistent with the finding that kestrels breeding in the centre of Warsaw had more female offspring (Rejt et al. 2005). The mortality of nestling Montagu's harriers (*Circus pygargus*) has also been shown to be biased, with smaller males most likely to die, especially if they hatch later in the season (Arroyo 2002). Our results do not necessarily imply a manipulation of the sex ratio but could relate simply to a greater susceptibility of the smaller (male) chicks when food resources are scarce.

3.3. Prey availability and diet choice

Rodents provide a higher nutritional value than avian prey (Goodwin 1980; Kirkwood 1991). Our survey of small mammals suggests that rodents are abundant in the city centre and the out-

skirts of Vienna but most species are nocturnal and thus hardly accessible to a diurnal raptor. Unlike the lesser kestrel *F. naumanni*, which is known to hunt during the night under artificial lighting (Negro et al. 2000), the kestrel is a largely diurnal hunter. Urban kestrels thus have to fly longer distances of at least several kilometres to hunt for their preferred prey (Riegert et al. 2007a; Riegert et al. 2007b). In the centre of larger cities it may be energetically preferable to switch to less profitable but more common avian prey (Korpimäki 1985). Indeed, recent studies indicate that kestrel populations in some larger European cities are increasingly feeding on birds (Kübler et al. 2005; Piattella et al. 1999; Quere 1990), whereas kestrels in smaller or medium-sized European cities rely largely on a diet of voles (*Microtus* sp.), as do their rural conspecifics (Rejt 2001; Riegert et al. 2007a; Romanowski 1996). In general, kestrels are believed to feed on what is locally abundant, although there have been reports of consistent differences in diet composition between neighbouring breeding pairs, presumably reflecting individual preferences for prey or differing abilities at catching different prey types (Costantini et al. 2005).

The increased proportion of non-rodent prey in kestrel pellets from the centre of Vienna compared with those from nearer the edge of the city is evidence that the birds generally hunt in the surroundings of their nest sites. Consistent with this idea, nest sites are often located close to green courtyards. A comparative study on generalist and specialist avian predators under fluctuating food conditions has shown that a vole specialist (pallid harrier *Circus macrourus*) forages less efficiently in poor vole years because the species is less efficient at capturing alternative prey, such as birds (Terraube et al. 2011). The increased effort required to hunt non-rodent prey may affect the breeding success of kestrels in the centre of Vienna. Our data indicate a trade-off between the ready availability of breeding cavities and the greater distances to hunting grounds, which result in a shift in the main prey taken and a lower breeding success.

Are inner-city buildings ecological traps for an urban raptor?

The kestrel is not truly an urban species. Although it has a strong preference for breeding in cavities, it does not profit from other human resources, nor does it show a higher degree of sociality and sedentariness (Kark et al. 2007). It clearly exploits the urban environment but high breeding densities in human-dominated landscapes do not necessarily indicate that the species benefits in terms of breeding success. Our findings are consistent with a trade-off between the availability of building cavities, which offer nest sites that are protected from potential predators, and the poorer food supply in the city centre. The consequence is that kestrels appear to select nest sites that are associated with increased reproductive failure and smaller fledged broods.

It may be difficult for kestrels to evaluate food availability when they are prospecting for nest sites (Hollander et al. 2013; Török et al. 2004 and citations therein) and errors could cause

birds to overestimate the quality of the habitat (Hollander et al. 2013; Kloskowski 2012) and settle in poor habitats despite the availability of better options. The preference for poorer habitats is a maladaptive behaviour associated with so-called ecological traps (reviewed in Battin 2004; Kokko and Sutherland 2001; Kristan 2003; Robertson and Hutto 2006; Schlaepfer et al. 2002). The idea that kestrels are falling into an ecological trap should be further investigated as it could be of conservation concern and might have important consequences for the viability of certain populations.

3.4. Conclusions

In the centre of Vienna, Austria, kestrels frequently breed in roof openings in historical buildings, a structural feature that is not available in the outskirts of the city. A comparison along the urban gradient shows the smallest nearest neighbour distances for pairs that breed in the city centre. The kestrel's favoured prey is rodents but in the centre rodents are less abundant and largely nocturnal and thus not available to diurnally hunting raptors. Kestrels breeding in the centre of Vienna consume more birds, including pigeons, and fewer rodents than kestrels in the outskirts. The city-dwelling raptor pays a high price for life in the city, with a lower reproductive success than birds breeding in the outskirts. The kestrel might appear to be an urban exploiter but given the poor reproductive performance of urban kestrels it is likely that the species is falling into an ecological trap. Although the kestrel is not itself of conservation concern, our findings suggest that other city-dwelling species may be faring less well than their abundance in the urban environment would appear to indicate.

4. Methods

4.1. Study system

The Eurasian kestrel, hereafter simply referred to as the kestrel, is the most abundant raptor in Vienna, Austria (48°12'N, 16°22'E; 415 km², ca. 150 – 500 m a. s. l., 1.8 million inhabitants). The estimated population density of 60-96 breeding pairs per 100 km² (Wichmann et al. 2009) is high compared to that in other European metropolises (e.g. Kupko et al. 2000; Malher et al. 2010) and in rural eastern Austria (Gamauf 1991). Kestrels return to Vienna at the end of March, before pair formation, and remain at their breeding sites until late summer (pers. obs. PS and AG). The study period covered three breeding seasons from March 2010 to August 2012.

The river Danube, lined with riparian forest, divides Vienna in two, making distance from the city centre misleading in terms of defining an urban gradient. We thus define urbanization by the percentage of sealed soil (calculated in ArcGIS 10 by ESRI ©, based on land covered by buildings or areas used by traffic on a land allocation map, digitized in 55 categories of land utilization between 2007 and 2010, in a circle of radius 500 m around the nest sites; *sensu* Zuckerberg et al. 2011). Areas with < 1% of unsealed soil were defined as rural and ex-

cluded from the analysis. Excluding these surroundings, mostly forested and agricultural areas, the urban study area covered 243 km² (Fig 1). Nests were distributed between percentages of sealed soil of 18% (most suburban) and 89% (most urban). By extending our search up to 1% soil sealing we made sure that NNDs were accurate.

With the help of local media we called on the public to report kestrel nests in Vienna in 2010 and 2011. Additionally, 25 volunteer ornithologists and PS and AG systematically searched the city for nests. Historic nest sites recorded in the BirdLife Austria archive ($N=103$), occupied nests found during systematic searches ($N=124$), locations of kestrel foundlings in the database of the animal shelter and the bird clinic at the University of Veterinary Medicine, Vienna ($N=78$) and nest sites reported by the general public were confirmed through personal observations during pair formation and courtship and classified as occupied if adults were present on two consecutive visits. During the study period we built a data base of 451 recent nest sites, between 50% and 65% of which were occupied each year.

4.2. Nest site and habitat parameters

Two different spatial levels were used to define nest site and habitat parameters. The percentage of sealed soil was calculated in a circle of $r=500$ m around the nest site (78.5 ha) and expressed as the percentage of land covered by buildings or areas used by traffic. The resulting value is termed the urban gradient. The distance (in m) from the nest site to the nearest open green space was recorded. The size of the nearest open green space, which was either a green courtyard or a park area in the city centre or a lawn (usually in a garden), a meadow or agricultural land in the suburbs, was assigned to one of four categories, ≥ 1 ha, ≥ 0.5 ha, ≥ 0.25 ha and ≥ 100 m².

We also described the building on which the nest was located, recording the nest height (m), façade structure, presence of roof openings or other cavities and presence of green courtyards (between 0.01 and 0.1 ha). We counted the stick nests of crows on the façade and in surrounding trees, as well as the number of window boxes on balconies. The same parameters were measured for 240 buildings chosen at random by placing a 500x500 m grid over the study area and using each intersection that touched a building. We used the height of the attic as hypothetical 'nest height' variable (as 62% of actual nest sites were located at attic level).

Habitat data were obtained via a land allocation map (1:7,500, resolution 15 cm), digitized based on geo-referenced aerial images provided by the Environmental Protection Bureau of Vienna (MA22-709/2010). Data on building structure were acquired on site.

4.3. Breeding parameters

Occupied nests that were accessible via the attic or by climbing were monitored 4-6 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, 157 broods were examined (36

nest sites in 2010, 52 in 2011 and 69 in 2012). Kestrels start incubation after the second egg is laid and the date (variable 'laying date') was estimated either directly or by subtracting 30 days from the estimated date of hatching (Village 1990). We defined 1 April as day 1 of the breeding season and numbered all dates of nest inspection thereafter for analysing survival (in total 118 days, see (Rotella et al. 2007) for methodological details). We used the residuals of layingdate and study year (calculated in an ANOVA with study year as predictor and laying date as predicted variable) to compare differences along the urban gradient. Additional covariates for nest survival models were percentage of sealed soil (%), age at which the nest was found, distance (m) from the closest open green space (area ≥ 1 ha) as a potential large hunting ground, presence/absence of a green courtyard (between 0.01 and 0.1 ha) within $r=100$ m from the nest site (factor variable 1/0) as a potential small hunting ground, area used by traffic (m^2 , in a circle of $r=100$ m around the nest site) as an indicator of noise disturbance and the NND (m) to the next active kestrel nest. In two years we additionally recorded for a larger data set ($N=200$ nests in 2010 and $N=185$ nests in 2011) the dates kestrels arrive at their nest sites: the information was provided by ornithologists involved in the breeding bird survey and observers living in direct view of a nest site. Involving the general public allowed us to have observers at accessible nest sites (mostly across the street or 'owners' of occupied window and nest boxes), who provided immediate information on hatching. In other cases we estimated the date of hatching from clutch initiation or egg floating. We marked chicks after hatching with non-toxic ink until they were ringed.

During repeated monitoring, the nestlings were measured, weighed and ringed (with rings from the Ringing Centre Radolfzell, Germany) when they were at least 10 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 and Kostrzewa 1993). We determined clutch size, hatching and fledging rates and size of the fledged brood (breeding success) for each nest. The hatching rate was recorded on a continuous scale from 0 (no eggs hatched) to 1 (all eggs hatched). The fledging rate was defined similarly and varied from 0 (no hatchling survived) to 1 (all hatched young successfully fledged). 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), so we considered pairs successful if they produced at least one 28-day-old chick. The size of the fledged brood was therefore the number of nestlings in successful nests at week 4.

Nests were defined as having failed if there was clutch loss during incubation or if all chicks died after hatching (as a result of predation, starvation, parasite infestation or parental abandonment). We attributed the cause of failure to abandonment if the nest contained intact and cold eggs and no adults were present during two subsequent inspections over 1-2 weeks

(*sensu* Strasser and Heath 2013) and to predation if predation was observed (crows robbing the nest during the day or broken eggs and marten tracks found in the breeding niche).

4.4. Sexing chicks

Sexing of chicks was based on the CHD system, Intron A (Griffiths et al. 1998). We used the blastoderm or embryonic tissue from unhatched eggs, buccal swabs (Wellbrock et al. 2012) for small nestlings (2-10 days) and blood of pinned growing feathers for older nestlings (>10 days). DNA was extracted with the QIAGEN DNeasy Blood & Tissue Kit following the standard protocol with Proteinase K. Sex was determined based on the 2718R and 2550F primer set (Fridolfsson and Ellegren 1999) and confirmed with the *Falco*-specific *fp102* and *fp49* primers (Nesje and Røed 2000). PCR amplification was performed in 25 µl containing 0.5 µl 10 mM dNTP, 0.25 µl of each forward and reverse primer (50 pmol/µl), 0.25 µl Dynazyme Polymerase and 2.5 µl 10x reaction buffer. PCR was performed with 40 cycles of 2 min at 94°C, 20 s at 50°C and 40 s at 72°C followed by 5 min at 72°C. PCR products were visualized on 2% agarose gels. The primary sex ratio was defined as the sex ratio in the full clutch (recorded in 2011 and 2012). The secondary sex ratio was defined as the sex ratio at fledging (recorded in all years).

4.5. Pellet analysis and abundance of prey

In 2010 and 2011, 637 pellets and remains of prey were collected from 37 different nest sites. We grouped the findings at nest sites according to their location along the urban gradient (*sensu* Kübler et al. 2005), distinguishing between city centre (288 pellets, $N=18$ nests with 81-89% sealed soil), mixed zone (206 pellets, $N=10$ nests, 51-80% sealed soil) and suburban areas (143 pellets, $N=9$ nests, 18-50% sealed soil). The pellets were dissected and prey remains classified as 'mammals', 'birds', 'reptiles' or 'insects'. We identified prey to species 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) and present data as their estimated biomass [g]: 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 (Arroyo 1997; Glutz von Blotzheim and Bauer 1980). Diet breadth (B) was calculated according to Levin's index (Levins 1968) as $B = 1/\sum p_i^2$, 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 assess the availability of potential avian prey in 2010, a team of 25 ornithologists monitored 25 transects ($N=9$ in the city centre, $N=9$ in the mixed zone and $N=7$ in suburban areas) in the course of the Austrian breeding bird survey using the standard method of 5-minute point-counts in the early morning under stable weather conditions (Südbeck et al. 2005). The ornithologists were recruited by Birdlife Austria and by PS. Each bird recorded within 50 m of the

point was identified based on voice and/or appearance. Analysis was based on prey known from pellet analysis (Sumasgutner et al. 2013) to be taken by kestrels. Potential prey was grouped by size (sparrow-, thrush- and pigeon-sized). Transects were selected by PS in ArcGIS 10 based on the land allocation map and included buildings, areas used by traffic, green courtyards (between 0.01 and 0.1 ha) and parks (between 0.3 and 600 ha) in the city centre and the mixed zone, and gardens and forest edges in the suburban area. Transects were chosen independently of the location of kestrel nests. They were sampled twice per year, at the beginning of the breeding season (in spring, calendar week 17-18, in April) and during the nestling period (in summer, calendar week 22-23, in June). Each transect consisted of 12-20 points at 300-500 m intervals.

The kestrel nest sites were assigned to the closest transects (max. distance 1 km, $N=2-24$ nests/transect). It is logical to allocate a nest to a transect rather than to a point as two or more count points could be within the hunting grounds of a single pair of kestrels. Furthermore, the assignment takes into account the spatial autocorrelation of neighbouring counting points on a transect. The proportion of successful breeding attempts was calculated for each transect and the figures were used to relate breeding success to availability of prey.

Densities of rodents were estimated by means of the 'minimum number alive method' of (Krebs 1996). We used 97 Rödl-type live traps (Janova et al. 2010) in 59 transects, with 10-20 traps in each of 23 different city parks (between 0.3 and 600 ha) across the urban gradient. The traps were checked twice per day (morning and evening) on two consecutive days per area at the start and the end of the 2010 breeding season, resulting in 2,676 trapping events (see (Mitter 2012) for details).

4.6. Statistical analysis

Differences in habitat between nest sites and buildings chosen at random were evaluated with a generalized linear model (GLM) with binomial error structure and a logit link function. The variables were nest height, facade structure, presence of roof openings or other cavities, and presence of green courtyards. One variable, houses with alcoves, was excluded because there were more roof openings in houses with alcoves (χ^2 -test, $N=248$, $df=1$, $P<0.001$) and the variable 'roof openings' was obviously related to nest site and thus of higher biological significance.

To analyse the relationship between abundance of prey and breeding success, a GLM was constructed with proportion of successful nests as dependent variable and the two predictors 'avian prey counted' and 'rodents trapped'. To calculate the proportion of successful nests we used the number of successful and failed nests per transect together as response variable fitted to a binomial error distribution. This can be treated as a weighted regression using the individual sample sizes as weights and the logit link function to ensure linearity (see Crawley 2007 for details).

All distance and area variables were logarithmically transformed. Analysis of the variation of breeding parameters with the urban gradient was performed by generalized linear mixed models (GLMM) with the `lmer` and `glmer` functions of the R package 'lme4' (Bates and Maechler 2009), including the nest site ID and the study year as random factors. Error distribution was chosen according to the response variable: Gaussian distribution and the identity link function for laying date and date of arrival at the nest site; binomial distribution and the logit link function for rates of hatching and fledging (values between 0 and 1); and Poisson distribution with the log link function for the sizes of the clutch and the fledged brood.

Models including soil sealing (urban gradient), NND (nearest neighbour distance) and laying date (timing of breeding) as explanatory variables were evaluated, as was a model including interactions between these variables. All explanatory variables were fitted to a maximal model and removed one by one, with the associated changes in the model deviance assessed by a likelihood ratio test (Zuur et al. 2009). After each step we calculated the AIC_c (Akaike Information Criterion, corrected for small sample sizes) and defined the model with the lowest value as the final one (Burnham et al. 2011). Model selection and model weight is presented in supplementary material 1. The proportion of deviance explained (%) for each fixed effect of the `lmer` models was analysed with the 'LMER Convenience Functions' package (Tremblay and Ransijn 2013). As this function has not yet been implemented for `glmer` models (`lme4` requires binomial and Poisson error distributions) we assessed estimates of variance explained using R^2 values, following the method recently described by (Nakagawa and Schielzeth 2013), implemented in the 'MuMIn' package (Barton 2013). To analyse nest survival we used the 'nest' model in 'RMark' (Laake et al. 2013; White and Burnham 1999). We considered models with $\Delta AIC < 2.0$ to represent good candidates (Krebs 2004). All statistical analysis was performed with the software R version 3.0.1 (R Development Core Team 2013).

4.7. Ethical notes

The study was performed under license from the Ethics Committee of the University of Veterinary Medicine, Vienna and the Environmental Protection Bureau of Vienna (MA 22/1263/2010/3). All sampling was conducted in strict accordance with current Austrian and EU law and followed the Weatherall Report and the guidelines for the treatment of animals in behavioural research and teaching (ASAB 2012).

Availability of supporting data: Morphological data on kestrels have been provided to the Ringing Centre in Radolfzell, Germany. Data from the breeding bird survey have been made available to Birdlife Austria and the Environmental Protection Bureau of Vienna (MA22) for use in conservation measures. All supporting data are available from the authors on request.

Abbreviations: Akaike Information Criterion, corrected for small sample sizes (AIC_c), generalized linear model (GLM), generalized linear mixed models (GLMM), nearest neighbour distance (NND).

Competing interests: The authors declare that they have no competing interests.

Authors' contributions: The original idea and study design came from PS, AG and HWK. PS performed the field and laboratory work; help by others is accordingly acknowledged. PS, EN and GT analysed the data. The manuscript was prepared by PS, EN, GT and AG and approved by all authors.

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Supplementary Material 1: Model selection for Table 2b in results section (dependence of breeding parameters on urbanization). Models are ranked according to the Akaike Information Criterion, corrected for small sample sizes (AIC_c). The ΔAIC_c indicates AIC_c differences between a particular model and the best-fitting model with the smallest AIC_c . Akaike weights (ω_i) indicate the contribution of each model to the average of all candidate models and K the number of parameters. Variables included in and excluded from a particular model are indicated by 1s and 0s, respectively. Id – laying date, ss – sealed soil, NND – nearest neighbour distance. Good candidate models are printed in bold.



Table 2b	Variables included			Model selection based on AIC_c			
	Id [‡]	NND [‡]	ss	K	AIC_c	ΔAIC_c	ω_i
Clutch size							
Final model	1	0	0	4	516.00	0	0.40
	1	0	1	5	517.00	1.02	0.24
	1	1	0	5	518.10	2.10	0.14
	1	1	1	6	518.90	2.95	0.09
	0	0	0	3	520.00	4.08	0.05
	0	0	1	4	520.30	4.34	0.05
	0	1	0	4	522.10	6.15	0.02
Full model	0	1	1	5	522.40	6.46	0.02
Hatching rate							
Final model	1	0	1	5	187.00	0	0.61
	1	1	1	6	189.10	2.05	0.22
	1	0	0	4	190.40	3.41	0.11
	1	1	0	5	192.50	5.49	0.04
	0	0	1	4	194.20	7.22	0.02
	0	1	1	5	196.30	9.25	0.01
	0	0	0	3	199.50	12.44	0
Full model	0	1	0	4	200.80	13.76	0
Fledging rate							
Final model	1	0	1	5	117.20	0	0.27
	1	0	0	4	117.60	0.38	0.23
	0	0	1	4	118.60	1.40	0.14
	1	1	1	6	118.80	1.63	0.12
	0	0	0	3	119.50	2.35	0.08
	1	1	0	5	119.60	2.46	0.08
	0	1	1	5	120.50	3.30	0.05
Full model	0	1	0	4	121.70	4.49	0.03
Fledged brood size							
Final model	1	0	1	5	628.80	0	0.47
	1	1	1	6	629.00	0.25	0.41
	1	0	0	4	632.20	3.46	0.08
	1	1	0	5	633.70	4.97	0.04
	0	0	1	4	647.90	19.14	0
	0	1	1	5	649.40	20.69	0
	0	0	0	3	654.00	25.21	0
Full model	0	1	0	4	656.10	27.31	0





Note: [‡] data presented as residuals with the study year, [‡] log transformed

Supplementary Material 2: Breeding parameters of *Falco tinnunculus* in Vienna, Austria, 2010-2012 ($N=157$ nest sites in total) in three urban zones. Results are shown as mean value \pm *SD*. We pooled those nest sites according to their location along the urban gradient (city centre with 81%-89% soil sealing, mixed zone with 51-80% soil sealing, and suburban area with 18-50% soil sealing).

	City centre	Mixed zone	Suburban area
2010 ($N=36$, in total 251 occupied nests within the urban study area)			
Laying date (first egg)	May 4 \pm 6.3 d (April 27)	May 3 \pm 11.9 d (April 15)	Mai 1 \pm 17.6 d (April 11)
Clutch size	2.52 \pm 2.06	4.58 \pm 1.73	5.00 \pm 1.41
Hatched	1.74 \pm 1.94	3.58 \pm 1.78	4.40 \pm 1.14
Fledged per breeding attempt	1.00 \pm 1.33	1.58 \pm 1.31	4.00 \pm 1.22
Fledged per successful pair	2.38 \pm 0.92	2.38 \pm 0.74	4.00 \pm 1.22
% successful pairs	42.11% ($N=8$)	66.67% ($N=8$)	100.00% ($N=5$)
2011 ($N=52$, in total 297 occupied nests)			
Laying date (first egg)	May 4 \pm 14.4 d (April 7)	May 3 \pm 15.1 d (April 6)	April 19 \pm 7.2 d (April 8)
Clutchsize	3.88 \pm 1.86	4.46 \pm 1.48	5.75 \pm 1.16
Hatched	2.38 \pm 2.42	3.57 \pm 1.89	4.25 \pm 2.71
Fledged per breeding attempt	1.81 \pm 1.94	2.61 \pm 1.79	3.50 \pm 2.39
Fledged per successful pair	3.22 \pm 1.39	3.32 \pm 1.29	4.67 \pm 1.21
% successful pairs	56.25% ($N=9$)	78.57% ($N=22$)	75.00% ($N=6$)
2012 ($N=69$, in total 215 occupied nests)			
Laying date (first egg)	May 4 \pm 11.3 d (April 12)	May 4 \pm 15.8 d (April 5)	April 24 \pm 16.42 d (April 4)
Clutch size	3.47 \pm 2.45	4.42 \pm 1.65	5.00 \pm 0.93
Hatched	2.83 \pm 2.21	3.58 \pm 2.11	4.13 \pm 1.88
Fledged per breeding attempt	2.48 \pm 1.95	2.81 \pm 1.99	3.53 \pm 2.10
Fledged per successful pair	3.80 \pm 1.21	3.95 \pm 0.95	4.42 \pm 1.16
% successful pairs	65.22% ($N=15$)	70.97% ($N=22$)	80.00% ($N=12$)

Supplementary Material 3: Nest site and habitat parameters used for statistical analysis.

Habitat parameters	Detailed description
Urban gradient	<p>percentage of sealed soil (%), based on land covered by buildings or areas used by traffic calculated on a land allocation map (1:7,500, resolution 15 cm), digitized in 55 categories of land utilization between 2007 and 2010, in a circle of radius 500 m around the nest sites and random points</p> 
City centre	81%-89% sealed soil
Mixed zone	51-80% sealed soil
Suburban area	18-50% sealed soil
NND	m, nearest neighbour distance to the closest active kestrel nest
Distance to nearest open green space	m, assigned to four different size categories, ≥ 1 ha, ≥ 0.5 ha, ≥ 0.25 ha, ≥ 100 m ²
Traffic area	<p>m², measured in a circle of radius 100 m around the nest site as an indicator for noise disturbance</p> 

Nest site parameters	Detailed description
Height	m, height of the nest site or height of the attic as hypothetical 'nest height' variable (as 62% of actual nest sites were located at attic level)
Facade structure	<p>presence/absence of stucco work</p> 
Roof openings	<p>presence/absence of specific architectural element (generally on buildings dating from pre-1940, especially from the so-called 'Gründerzeit' between 1848 and 1873) in the historic districts of Vienna, located between the highest row of windows and the roof; 24-62 cm in width, 16-50 cm in depth and 24-48 cm in height</p> 
Other building cavities	<p>presence/absence, matching the size of a suitable breeding cavity</p> 
Green courtyard	<p>presence/absence, size between 0.01 and 0.1 ha</p> 

Part 1

Chapter II: Sumasgutner P, Schulze CH, Krenn HW, Gamauf A (2014) Conservation related conflicts in the nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey. — Landscape and Urban Planning. doi:10.1016/j.landurbplan.2014.03.009.



Photo: Heinrich Frötscher

Conservation related conflicts in nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey

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Highlights

- The city of Vienna, Austria, has a large urban Eurasian kestrel population.
- Kestrels prefer breeding in roof-openings on historical buildings in the center.
- Kestrels seem to hunt in their immediate surroundings, like backyards and city parks.
- A high proportion of avian prey negatively influences breeding success.
- The choice of the urban habitat is associated with reduced reproductive rates.

Abstract

The urban space is a permanently changing ecosystem, suffering from decreasing biodiversity, but also providing new anthropogenic habitats for some adaptable species. The Eurasian kestrel (*Falco tinnunculus*) is such an adaptable species, whose dense urban populations are ethologically different from rural populations in Europe. Several studies have indicated that urban kestrels increasingly prey on birds; this study even indicated avian prey as the main prey category

in the inner-city habitat. We analyzed the selection of habitat and building structure parameters while controlling for differences in their availability in Vienna, Austria, a city of 1.7 million inhabitants. We then connected the nest-site selection of urban kestrels to their diet choice and annual reproduction rate. Our results indicated a trade-off between higher nest-site availability in the center and longer distances to larger open green space as optimal foraging ground. Between 2010 and 2012, a preference for breeding in close vicinity to green backyards was linked to earlier laying dates, higher hatching rates and larger fledged brood sizes, but the overall productivity per nest still remained low in the center compared to the suburban area. In a survey of avian prey species, we found comparable abundances of prey-sized bird species in green backyards, parks and surrounding suburban areas. We thus hypothesize that kestrels use the immediate nest-surroundings to hunt, but are not as efficient in hunting avian prey as they are in hunting voles. Changes in modern city architecture and renovation of historical buildings pose conservation related threats to urban predators and prey.

Keywords: Urbanization, Avian community, Predator-prey interaction, Nest-site selection. Cavity breeders, *Falco tinnunculus*

1. Introduction

The urban space is a permanently and rapidly changing ecosystem (Magle et al. 2012) characterized by progressive impervious surfaces, lower proportions of green space and the conversion of original vegetation or farmland to parklands or backyards (Er et al. 2005). Although many bird species decline once an area is urbanized, other species take advantage of the opportunities and the altered patterns of predation and competition that accompany a shift in assemblage composition (Catterall 2009). Several raptors benefit from urbanization, with over 25 species living in urban settings (Love and Bird 2000), although in general species richness of carnivores tends to decrease in urbanized areas (Reis et al. 2012). Some specialized diurnal raptors suffer from increasing urbanization, while generalists are less affected and even thrive (Sorace and Gustin 2009). Particularly species with smaller home ranges cope well with habitat reduction, whereas raptors with large home ranges are more negatively affected, although some species respond with higher reproductive success to urban environment (Bird et al. 1996). This is linked to their ability to utilize artificial nest-sites, for example buildings (Chace and Walsh 2006). However, it is unclear to which extent young birds raised in artificial nest-sites are imprinted to these (Kleinstäuber et al. 2009) and to the urban nesting habitat, since settlement in natal-like habitat may explain maladaptive habitat selection in some species (Piper et al. 2013). Human activities affecting nest-sites, for example changes in architectural style, could negatively affect individual survival or even the whole breeding population. Consequently, currently common and well-adapted raptor species that prefer buildings as nest-sites in metropolitan areas may come under threat in the future (e.g. Mikula, Hromada and Tryjanowski 2013).

One fairly common and adaptable raptor species is the Eurasian kestrel (*Falco tinnunculus* Linnaeus, 1758). It is an excellent model for an urban top-predator. Predators are an integral part of any ecosystem; a diverse predator community may indicate a healthy ecosystem (Sorace and Gustin 2009). Plus, the kestrel can be used as 'flagship' species to inspire public interest and goodwill for conservation action. The kestrel has presumably been associated with cities and humans for as long as they have existed; the first documents of urban kestrels date from 19th century London (Cramp and Tomlins 1966). Although a number of studies about breeding biology and diet were conducted in the last decades, e.g. in Munich (Kurth 1970), Prague (Plesník 1991), Bratislava (Darolová 1992), Rome (Salvati et al. 1999), Warsaw (Rejt 2001) and Berlin (Kübler et al. 2005), many questions about architecture dependent nest-site quality associated with breeding and feeding ecology remain unresolved. Compared to rural kestrels, urban populations may also be behaviorally and even genetically different (Riegert et al. 2010; Rutkowski et al. 2006). For example, recent studies indicate that kestrels in larger Central European cities increasingly feed on birds (Kübler et al. 2005; Piattella et al. 1999).

Due to the inability of falcons to build a nest platform, the availability of suitable nest-sites seems to be a limiting factor to their breeding occurrence (Newton 1979). The most commonly used sites are abandoned stick-nests of other bird species in trees and ledges on buildings. Any structure that provides protection from predators, is sheltered and can hold eggs is a potential nest-site (Village 1990); this includes attics or window-boxes in high-rise flats (Charter et al. 2007). In other cities, kestrels face a diminishing number of nest-sites on buildings due to widespread refurbishment works; making artificial nest-boxes increasingly important (Mannan et al. 2000). For conservation of kestrel populations, one must understand costs and benefits of urban breeding, like higher nest-site availability and lower predation risk versus more remote foraging grounds (Riegert et al. 2007; Tella et al. 1996) and the risk of collisions with windows and vehicles (Chace and Walsh 2006). To date, several studies on urban kestrels have reported higher breeding success (overview in Charter et al. (2007) with the exception of Kübler et al. (2005) and Sumasgutner et al. (2013).

In Vienna, Austria, the estimated population density of 60-96 breeding pairs (bp)/100 km² (Wichmann et al. 2009) is high compared to other large European cities with estimates between 23 and 55 bp/100 km² (Kübler et al. 2005; Malher et al. 2010). Recently detected differences in annual reproduction rates showed a substantially higher rate of nest failure, mostly associated with nest desertion and predation, in the city center (Sumasgutner et al. 2013). These differences in the breeding system clearly called for further investigation. In this paper, we aim to analyze habitat and nest-site characteristics which could be related to lower breeding success in the center. For this purpose we compare landscape composition and the specific building structure chosen by kestrels to randomly selected areas and random buildings to (1) identify habitat and nest-site parameters attracting kestrels to inner-city areas. We further test the influence of (2) habitat and nest-site features on breeding success. Diet analyses of urban breeding kestrels in our previous work further highlighted the importance of avian prey as an alternative to small mammals (Sumasgutner et al. 2013). Therefore, we investigated (3) the abundance of avian prey in different urban habitat types relating to breeding success. Finally we discuss (4) conservation strategies to be derived from kestrels' preferences in the urban environment.

2. Materials and methods

2.1. Study area and study design

The study was performed in Vienna, Austria (48°12'N, 16°22'E; 415 km²), a city of 1.7 million inhabitants. Vienna is known as a green city; about 49% of its surface is unsealed soil (Berger and Ehrendorfer 2011). We defined the urban area as landscape with > 1% impervious surfaces (size of urban study area 243 km², scale 1:7 500, resolution 15 cm, Fig. 1). We used historical (from the year 1775, Berger and Ehrendorfer, 2011) and recent land allocation maps (provided

by the Environmental Protection Bureau of Vienna, digitized in 55 categories of land utilization between 2007 and 2010) to define three urban zones: the city center (C – the old town in 1775, recent impervious surfaces of > 75%), the mixed zone (MZ – parts of the old town in 1775 located along the green riverside and surrounding former cultivated landscapes, recent impervious surfaces of 45-75%) and the suburban area (SA – recent outskirts of Vienna with impervious surfaces of <45%), and assigned each nest-site to one of these zones (Supplementary Material 1). The proportion of impervious surfaces was calculated for $r=500$ m around the nest-sites using ArcGIS 10 by ESRI© based on building densities and traffic areas.

2.2. Field work

2.2.1 The urban kestrel population

An effective and cost-efficient way to find an adequate sample size of nest-sites was to employ the help of the general public. A media relations campaign issued a public call to report kestrel nest-sites in the city between 2010 and 2012. Additionally, 31 ornithologists involved in the breeding-bird survey (see below) and the authors PS and AG systematically searched for nests. We confirmed the occupation of reported nest-sites through personal observations during pair formation and courtship. During the study period (2010-2012) we built a data-base with 451 recent nest-sites; between 50 and 65% of the nests being occupied each year.

Those nests accessible via the attic or by façade and tree climbing were monitored 4-6 times during each breeding season in 2010-2012 to determine (1) laying date, (2) clutch size, (3) number of hatched offspring and (4) number of fledged young. These detailed breeding parameters were available for 157 nests. The nestlings were measured, weighed and banded (ring from Radolfzell Ringing Center, Germany).

Hatching rate was defined between 1 if all eggs of the clutch hatched and 0 if no egg hatched, with the according values in between. The final inspection was conducted in the last week of the nestling period (between 24 and 30 days after hatching). Hence, the fledged brood size was the number of nestlings at week 4. We considered pairs successful if they produced at least one 28-day-old chick (Village 1990).

The urban kestrel data set also covered the nearest-neighbor-distances (NND, distance the nearest occupied nests in m) for the whole study period. Beside the detailed fledged brood sizes mentioned above we further knew for 2010 and 2011 the breeding outcome of occupied nests, quantified as successful (at least one fledged young) or failed.

2.2.2 Breeding-bird survey

Between 2010 and 2011 a field survey determined the abundance of potential avian prey for urban breeding kestrels. To capture the relative abundance of the bird population in both years, a team of 31 ornithologists monitored 33 point-count-transects (Supplementary Material 2).

Transects were sampled twice annually using the standard method of 5 min point-count-units (Bibby et al. 2000) with early morning counts under stable weather conditions. The first sample period coincided with the beginning breeding season (calendar week 17-18 in April), the second with the kestrels' nestling period (calendar week 22-23 in June). Each transect consisted of 12 to 20 points (distributed along 3.6 to 6 km), spaced evenly every 300-500 meters. During monitoring, each detected bird within 50 m from the point (see Newell, Sheehan, Wood, Rodewald, Buehler, Keyser, Dwas *et al.* 2013 for effectiveness of the method) was identified at species level by voice or sight. We ensured that the bird count points were distributed across the following habitat types to characterize the previously defined urban study area: city center (C - impervious surfaces of > 75%, $n=374$ point-count-units), green backyard (B - size between 0.1 and 0.25 ha, $n=259$) and park (P - size between 0.35 and 600 ha, $n=267$). In the outskirts we additionally separated gardens (G, $n=427$) and forests (F, $n=184$).

2.3. Video monitoring

The number of prey individuals found in kestrel pellets can misrepresent the percentage of certain prey categories being completely digested (Trierweiler and Hegemann 2011). Since vertebrate bones and invertebrates cannot be adequately identified by analyzing pellets, a quantitative assessment of diet composition is hardly possible. We therefore installed video-monitoring systems at three different nest-sites (one located in the C with 86% impervious surfaces in 2011, one in the MZ with 74% in 2010 and one in the SA with 35% in 2011). The cameras inside the brood-niche filmed the feeding process (Navigator Super Wireless mini-camera, with infra-red lighting and radio transmission to an external storage volume) continuously recording (software G01984) the whole nestling period (19 days between June 19 and July 7 in 2010 and 40 days between May 20 and July 3 in 2011). The biomass [g] of identified prey individuals was calculated based on Arroyo (1997) and Glutz von Blotzheim and Bauer (1980).

2.4. Habitat analyses

First we investigated the correlation between nest attempts and landscape composition and building structure variables, and second between nest success and landscape composition, building structure and NND. For this purpose we selected 240 random points (Fig. 1), allowing us to study habitat and nest-site selection while controlling for differences in habitat and nest-site availability (*sensu* Sergio *et al.* 2005, Tanferna *et al.* 2013). We placed a 500 m x 500 m grid over the study area map and randomly selected 240 crossings points (only considering those with >1% impervious surfaces within a radius of 500 m) as 'random points' used in habitat analyses. The sample size of 240 was chosen because it was the number of then known nest-sites to ensure an equal sample size of random points and nest-sites.

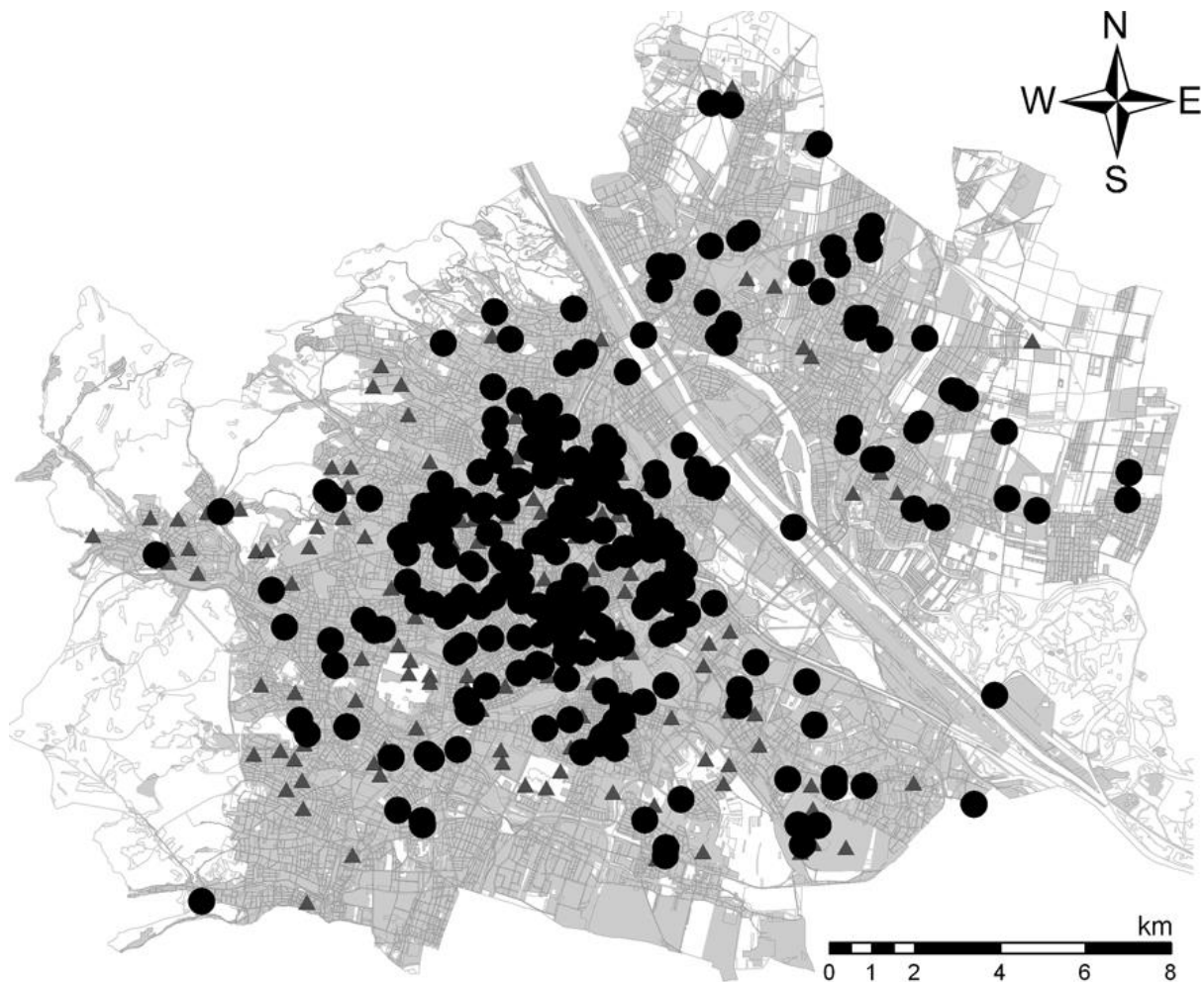


Fig. 1: Nest-sites of Eurasian kestrels (*Falco tinnunculus*) in Vienna in 2010 (black dots, $n=251$) located within the defined urban area (243 km², soil sealing > 1%, light gray) and random points (gray triangles, $n=240$).

2.4.1. Landscape composition and habitat analyses

The habitat was defined as the area within a radius $r=500$ m (78.5 ha) around the nest-site and the random points. Twelve different land use parameters were used to describe the relative composition of urban habitat: building areas, green backyards, lawns and meadows, agricultural land ('fields'), woodland ('forests'), cemeteries and vineyards, as well as the distance from the nest-site to the nearest open green space (in four size categories: > 1 ha, > 0.5 ha, > 0.25 ha, ≥ 0.01 ha). Occupied nest-sites were compared to 240 random areas (hereafter 'RA', in $r=500$ m around each random point). The scale of 500 m was chosen because it was the mean NND between kestrel nests over the whole urban study area and period. We do not have data on home range sizes of urban breeding kestrels in Vienna, but the chosen 78.5 ha were similar to the size of kestrel hunting areas reported from the cities Kiel, Germany (Beichle, 1980; range of 90–310 ha) and České Budějovice, Czech Republic (Riegert, 2007; range of 80–2500 ha).

2.4.2. Building structure and nest-site analyses

The random points resulted further in 478 randomly selected buildings (hereafter 'RB') for structure analyses. In most cases, the random point was located close to, but not exactly on a single building. Therefore we sampled each building adjacent to this point (between 1 and 4 buildings) – to avoid the sampling effect of unwittingly making a biased choice of one of the potential buildings. Data acquisition for both the actual nest-sites and the random buildings was done on-site, describing the immediate surroundings using eight variables: (a) building type (based on construction period: new building – built since 1945; old building – built before 1945; promoterism building – built around 1840; magnificent building – older than 19th century; school; council flat; church; family home), (b) orientation of nest-site or random building towards the observer, (c) height (m; we used the height of the attic as hypothetical 'nest height' variable since 62% of actual nest-sites were located at this level) and (d) façade structure (richness of stucco work: none, low, middle, high). Additionally, we counted available cavities as (e) the number of roof openings and (f) other niche structures. Roof openings are a specific architectural element in the historic districts (on old and promoterism buildings) of Vienna. The openings are located between the last row of windows and the roof, and measure between 24 and 62 cm in width, 16-50 cm in depth and 24-48 cm in height. We further recorded (g) the number of apartment conversions of attics of historic buildings to factor in the loss of brood niches due to this advancing trend. Finally, we noted (h) the presence or absence of green backyards as potential hunting ground in the immediate surroundings. At all accessible nest-sites, we additionally measured the size of the breeding-niche to calculate the available space (ground area and volume) for the brood.

2.5. Statistical analyses

We used generalized linear models (glm) and generalized linear mixed models (glmm) with the R package "lme4" (Bates and Maechler 2009), depending on the necessity of including the site ID and the study year as random factors. The error distribution was chosen according to the type of response variable: Binomial distribution and logit link function for occupation, successful vs. failed nests and the ratio of hatched offspring, Gaussian distribution and identity link function for laying date and Poisson distribution with log link function for clutch size and fledged brood size. When building glms and glmms, all explanatory variables were fitted to a maximal full model and simplified using backward elimination based on likelihood-ratio test and *F*-Statistics (Chisq-Statistics for models with binomial or Poisson error structure) and with $P < 0.05$ as the selection criterion ("drop1"-function in R) until reaching the minimum adequate model. Assumptions of all models were checked on the residuals of the final model. At each step, we calculated the AIC_c (Akaike Information Criterion corrected for small sample size), and considered as final model the one with the lowest value (Burnham et al. 2011). We present details

on the stepwise procedure with AIC_c , ΔAIC_c and according model weights (ω_i) as Supplementary Material 4-5. All statistical analyses were performed with the software R version 3.0.2 (R Development Core Team 2013), unless stated otherwise.

2.5.1. Occupation, breeding success and landscape composition parameters

Habitat differences between actual nest attempts (occupation data 2010-2012, $n=736$) and random areas ($n=240$), and between nest success vs. failure (2010 and 2011, $n=534$) were evaluated with glmms, including the site ID and study year as random factors. The influence of landscape composition parameters on fledged brood sizes (breeding data 2010-2012, $n=157$, presented for each study year separately) was analyzed with glms. In advance, we reduced macro-habitat variables by principal component analysis (PCA) with Varimax-rotation, due to multicollinearity of landscape composition parameters. The Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) indicated that our data were suitable for PCA ($n=12$, $KMO=0.86$; Bartlett-test for sphericity, $\chi^2=6\,676$, $P<0.001$, Budaev 2010). The PCA produced four principal components (PC1-4, Supplementary Material 3) with an Eigenvalue of ≤ 1 , explaining 74.9% of the variance. The full model included PC1-4 for occupation together with NND for nest success vs. failure and fledged brood sizes.

2.5.2. Breeding performance and nest-site parameters

First we tested whether the distribution of nest-sites significantly differed from the distribution of random buildings. Nest-site selection in structural variables was analyzed using Pearson χ^2 -tests. In the Pearson statistic, the χ^2 -value [$=\sum (\text{observed-expected})^2/\text{expected}$] is compared to a χ^2 -distribution with $m-1$ degrees of freedom, where m is the number of categories tested (e.g. number of building types, etc.). The critical P value of 0.05 in all 8 tests in 36 variables was adjusted using Bonferroni correction, i.e. $P=0.05/44=0.0011$. Second, since the Pearson statistic does not determine preference or avoidance of individual categories, we calculated 100 $(1-\alpha)\%$ simultaneous confidence intervals for the difference between nest-sites and RBs in each structure variable class (z -value $=3.285$, $\alpha=0.00051$; see Marcum and Loftsgaarden 1980 for details on the statistical method used).

To identify building structure variables influencing breeding time (laying date) and breeding parameters (clutch size, ratio of hatched eggs and fledged brood size), we performed glmms with site ID and study year as random factors. The full model included the following variables, provided that they were significant in single term comparisons: all building structure variables except attic conversion (see point 2.4.2. above), nest-type (building-cavity, façade-nest, planters, nest-box and tree-nest), ground area and volume in cavity-broods, the urban zone (C, MZ and SA), distance to the nearest open green space (size categories: > 1 ha, > 0.5 ha, > 0.25 ha, ≥ 0.01 ha) and NND.

2.5.3. Distribution of avian prey

To analyze the importance of birds as potential prey for kestrels, we pooled the species known to appear in kestrel pellets (Sumasgutner et al. 2013) into three size-classes (according to their biomass): size 1 - sparrow, size 2 - thrush, size 3 - pigeon. We excluded corvids and other large birds from the analysis, as they are not viable prey. We only included data from census points sampled twice in April and June in both years by the same person ($n=209$ census points). To assess differences in the prey size composition between urban habitat types, a dissimilarity-among-sites matrix was developed, using Bray–Curtis dissimilarities based on the mean number of bird individuals of each size-class observed at each census point (*sensu* White, Antos, Fitzsimons and Palmer 2005). The resulting study site matrix formed the basis for further analyses in Primer 5.2 (Clarke and Gorley 2001). To test whether size-class composition differed between urban habitat types, we performed a one-way ANOSIM (Clarke and Warwick 2001), with 999 random permutations on the similarity matrix for pooled data and for the spring and summer surveys separately. Glms (normal error distribution; log-link function) were calculated separately for each of the three bird size classes to test for effects of habitat, season and year (including all interaction terms) on the abundance of avian prey (Supplementary Material 6).

2.6. Ethical Note

The study was performed under license from the Environmental Protection Bureau of Vienna (MA22/1263/2010/3) and the ethics committee of the University of Veterinary Medicine, Vienna (BGBI.Nr.501/1989i.d.g.F.).

3. Results

3.1. Habitat use and habitat availability

Nest-sites of *F. tinnunculus* are located in areas characterized by higher building densities, higher numbers of green backyards and longer distances to open green space, but higher percentage of fields and lower forest cover compared to random areas in Vienna: The glmm testing for effects of the principal components (final model including PC1-4) combining 12 habitat variables shows a significant effect of PC1 (high factor loadings on variables correlated with building density and green space) and PC3 (high factor loadings on variables correlated with fields and forest) on nest-site selection (Table 1, see supplementary material 3 for details).

The glmm for discriminating between nest success vs. failure (binomial error distribution; logit-link function; data set 2010-2012) did not indicate any explanatory capacity of PC1-4 and nearest-neighbor-distances (non-significant results not shown). Of the breeding pairs, 43% were unsuccessful, failing to fledge at least one young, with significantly more failures in the city center ($n=$ a total of 56 nests failed; Fisher's Exact test: $P=0.02$).

Table 1: Dependence of occupation on the principal component scores of macro-habitat variables shown by glmms with binomial error structure and a logit function. Note that site ID and study year were used as random factors.

Occupied macro-habitats (2010-2012, $n=736$) vs. random areas ($n=240$)	Estimate	SE	Z-value	$Pr(> z)$	Sign.
PC1	2.60	1.24	2.09	0.0363	*
PC2	-3.03	2.35	-1.29	0.1985	NS
PC3	5.83	2.33	2.51	0.0123	*
PC4	1.94	2.68	0.73	0.4683	NS
(Intercept)	9.05	3.24	2.80	0.0052	**

Significance codes: '***' 0.01, '*' 0.05, 'NS' not significant.

3.2. Landscape composition and fledged brood size

Fledged brood sizes in all years were predicted by higher values of PC3 (Table 2), indicating higher fledging success at sites surrounded by fields but low forest cover. In 2012 we further found nests having lower fledging success in areas with higher building densities, higher percentage of green backyards and at greater distances from larger open green space (all variables with higher factor loadings on PC1), which is typical for the city center (Table 2).

Table 2: Dependence of fledging success (value 0-6) on the principal component scores of macro-habitat variables shown by glms with poisson error structure and a logit function.

2010 ($n=36$)					
Variable	Estimate	SE	Z-value	P-value	Sign.
PC3	0.38	0.15	2.55	0.0109	*
(Intercept)	0.51	0.15	3.31	0.0009	***
2011 ($n=52$)					
Variable	Estimate	SE	Z-value	P-value	Sign.
PC3	0.19	0.11	1.78	0.0746	•
PC4	0.28	0.15	1.89	0.0590	•
(Intercept)	0.87	0.10	8.60	<0.0001	***
2012 ($n=69$)					
Variable	Estimate	SE	Z-value	P-value	Sign.
PC1	-0.13	0.05	-2.77	0.0057	**
PC3	0.15	0.09	1.66	0.0961	•
(Intercept)	1.20	0.09	13.59	<0.0001	***

Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '•' <0.1.

3.3. Nest-site choice and nest-site availability

Nest-site monitoring in 2010 resulted in 251 breeding pairs (bp) within the urban study area with exact location of the nest-sites known (Fig. 1). In 2011, we located 297 bp and in 2012 we located 215 bp; this results in a breeding pair density ranging between 88.5 and 122.2 bp/100 km² in urbanized areas of Vienna. We found kestrels predominantly breeding on buildings (76.7% of full data-base with 451 different recent nest-sites), where they primarily used roof

openings (44.3%), other niche structures (12.0%) or corvid nests on the façade (8.2%). Secondly, they used abandoned nests on trees (20.2%). Nest-boxes played a minor role (5.5%), as there is no organized nest-box program currently implemented. Window-boxes were rarely used as nest-sites (6.7%). Therefore kestrels in Vienna are predominantly cavity breeders (61.9% of nest-sites located in enclosed niche structures), particularly in the center. During the study period, a total of 27 nest-sites (8.8%) were lost due to building renovations.

In five out of eight nest-site-related structure parameters, significant differences to random buildings were found after Bonferroni correction to $P \leq 0.0011$ (Fig. 2). Kestrels use most building types for nesting relative to their availability in the city (Fig. 2a). Most kestrels nest in old buildings (45.7% used, 57.9% available) and buildings from the period of promoterism (13.9% used, 11.1% available). Kestrels significantly avoid new buildings and family homes as nest-sites. No significant selection of a certain orientation was found (Fig. 2b). Most nest-sites were located in a height of 16 – 21 m (Fig. 2c, 40.9%). Significantly fewer nests were found in the height category 12 – 16 m, which is the predominant height class available (36.0%). No significant preference for a certain type of façade structure was found (Fig. 2d). Roof openings (Fig. 2e) and other niche-structures (Fig. 2f) positively affected the occurrence of breeding attempts. Kestrels particularly use roof openings for nesting (40.9% of all nests, 59.9% of nests on buildings), underlining their dependence on their accessibility or on the availability of other niche-structures. We did not find an effect of attic conversion on kestrels breeding on buildings (Fig. 2g). Kestrels significantly prefer breeding in the vicinity of green backyards and avoid sites without (Fig. 2h).

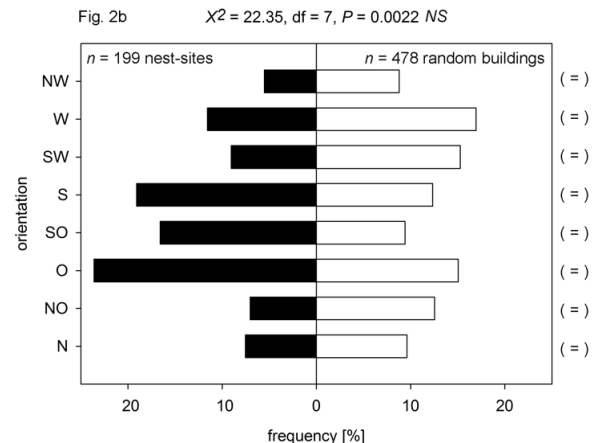
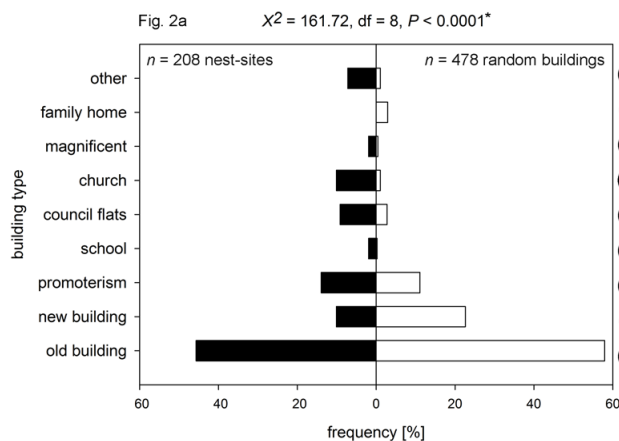
3.4. Building structure and breeding performance

Between 2010 and 2012 we examined the nestlings of 157 breeding pairs. Laying dates were earlier in cavities facing south. We further found earlier laying dates in close proximity to minor green space (≥ 0.01 ha, Table 3a). All breeding parameters significantly decreased with later laying dates (Table 3b). Clutch sizes were smaller in crow-nests on façades, but slightly larger on buildings bordering a green backyard. Further, hatching rates and fledged brood sizes were significantly higher at nest-sites located close to a yard. Fledged brood sizes were smallest in the inner-city habitats. Less young successfully fledged in crow-nests on façades, more in nest-boxes. In cavity breeders, we found no significant relationship between clutch sizes and ground area [cm^2] of the brood niche ($n=92$, glmm $z=0.13$, $P=0.21$), nor between fledged brood sizes and volume [cm^3] of the brood-niche ($n=97$, glmm $z=0.42$, $P=0.68$).

Table 3: Dependence of (a) breeding time and (b) breeding parameters (2010-2012, $n=157$) on building structure parameters as fixed effects (manual backward stepwise elimination procedure) in a generalized linear mixed model (glmm). We included the nest-site ID and the study year as random factors. Only the minimum adequate models are shown.

(a) Breeding time		Estimate	SE	T-value	$Pr(> t)$	Sign.
Laying date ($n=148$)						
Exposition	N	-2.82	4.28	-0.66	0.5112	NS
	S	-7.76	3.15	-2.46	0.0160	*
	W	-1.06	3.52	-0.30	0.7634	NS
Distance (m) [†] to green space (≥ 0.01 ha) [†]		6.91	2.29	3.02	0.0033	**
(Intercept)		29.00	3.57	8.12	<0.0001	***
(b) Breeding parameter		Estimate	SE	Z-value	$Pr(> z)$	Sign.
Clutch size ($n=129$)						
Laying date [‡]		-0.01	0.00	-2.56	0.0106	*
Brood in crow-nests (on the façade)		-0.33	0.14	-2.33	0.0200	*
(Intercept)		1.58	0.04	36.48	<0.0001	***
Ratio of hatched eggs ($n=157$)						
Laying date [‡]		-0.04	0.01	-2.85	0.0043	**
Presence of green backyard		0.94	0.36	2.63	0.0085	**
(Intercept)		0.08	0.27	0.29	0.7731	NS
Fledged brood size ($n=148$)						
Laying date [‡]		-0.01	0.00	-3.11	0.0019	**
Urban zone	Mixed zone	-0.38	0.17	-2.29	0.0220	*
	Suburban area	0.10	0.19	0.53	0.5988	NS
Exposition	N	0.35	0.20	1.75	0.0809	•
	S	0.18	0.14	1.32	0.1857	NS
	W	-0.15	0.17	-0.86	0.3903	NS
Nest-type	Crow-nest on the façade	-0.57	0.32	-1.77	0.0760	•
	Nest-box	0.33	0.19	1.77	0.0775	•
	Planter	0.20	0.19	1.08	0.2792	NS
Presence of green backyard		0.43	0.15	2.88	0.0039	**
(Intercept)		0.47	0.18	2.65	0.0080	**

Note: [†] data presented as residuals with the study year, [‡] log transformed
Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '•' <0.1, 'NS' not significant.



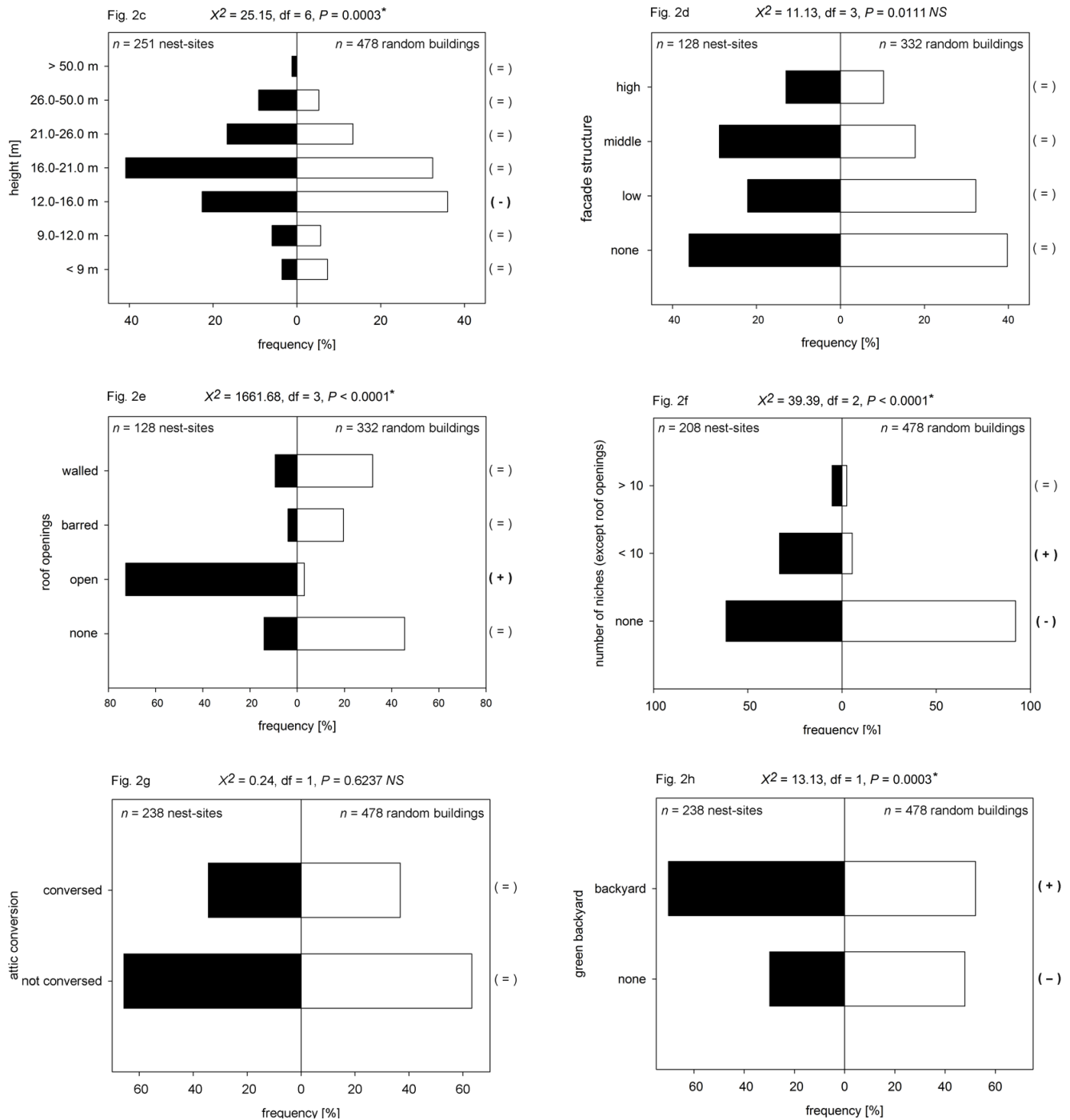


Fig. 2: Comparison of Eurasian kestrel nest-sites in 2010 (black bars, left side) and random buildings (white bars, right side) using Pearson χ^2 -tests and simultaneous confidence intervals. The number of nest-sites is expressed in %frequency (χ^2 -values and probabilities are presented, Bonferroni corrected significance level: P -values < 0.0011 are indicated with *). In each category, differences between the proportion of nest-sites and the proportion of random buildings are expressed by the terms: preference (+), no effect (=), avoidance (-).

3.5. Diet choice

We identified 1009 prey items by video-monitoring. The main prey category in the city center was avian prey with 70.6% of total biomass delivered to the nestlings ($n=63$ bird individuals),

followed by 28.5% rodents ($n=118$). In the mixed zone prey consisted of 30.1% avian prey, 60.0% rodents, 4.9% insects, 2.9% reptiles and 2.2% earthworms. In the suburban area (soil sealing 35%) the main prey category was rodents (98.9%, $n=155$). In total, most identified prey items on video material were insects ($n=516$) with only 2.1% biomass of prey consumed.

The most common mammalian prey was *Microtus* sp. (sub-sample size: $n=84$). We identified 92 bird individuals from 11 species. The most common species were sparrows (*Passer domesticus*, *P. montanus*, $n=9$), followed by black redstarts (*Phoenicurus ochruros*, $n=5$). We identified 12 feral pigeons (*Columba livia*) at the nest-sites in the C and in the MZ. The most common arthropods were grasshoppers, with at least 165 individuals.

3.6. Distribution of avian prey

During the breeding bird survey (pooled data from 2010 and 2011), we recorded 89 bird species ($n=1511$ point-count-units, 75 species in 2010 and 80 species in 2011).

Table 4: Results of ANOSIMs testing for effects of urban habitat type on the composition of the bird assemblage within 3 size classes (size 1- sparrow, size 2- thrush, size 3- pigeon) for pooled data 2010-2011; and for spring and summer separately. Urban habitat types considered: city center (C), green backyard (B), park (P), garden (G) and forest (F). Size similarity was quantified by Bray-Curtis similarities (based on square root transformed abundances).

Pairwise tests	2010 and 2011			Spring		Summer	
	<i>R</i>	<i>P</i> - value	Sign.	<i>R</i>	<i>P</i> - value	<i>R</i>	<i>P</i> - value
C vs. B	0.051	0.001	***	0.024	0.009	0.042	0.002
C vs. P	0.095	0.001	***	0.147	0.001	0.083	0.001
C vs. G	0.264	0.001	***	0.306	0.001	0.224	0.001
B vs. P	0.059	0.001	***	0.088	0.001	0.022	0.02
B vs. G	0.198	0.001	***	0.245	0.001	0.099	0.001
P vs. G	0.068	0.001	***	0.053	0.001	0.062	0.001
F vs. C	0.119	0.003	**	0.159	0.001	0.11	0.001
F vs. B	0.081	0.007	**	0.098	0.007	0.049	0.031
F vs. P	-0.046	0.941	NS	-0.053	0.955	0.002	0.439
G vs. F	-0.025	0.756	NS	-0.024	0.709	-0.021	0.722

Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '•' <0.1, 'NS' not significant.

The composition of birds (grouped into three defined size-classes) as potential prey differed between urban habitat types as indicated by ANOSIM analyses using Bray-Curtis dissimilarities to quantify differences in the composition of avifaunal size class distribution between census points (Table 4). Glms testing for effects of habitat, season and year on the abundance of birds of different size-classes indicated that abundance in all three size-classes was most strongly affected by habitat (supplementary material 6). The abundance of sparrow-sized birds in spring was lowest in the city center and increased towards green backyards, parks, gardens and forests. During the kestrel's breeding season abundance remained relatively low in the city center (Fig.

3). Also blackbird-sized birds showed lowest abundances in the city center in both seasons. In pigeon-sized birds we found the opposite pattern with highest abundances in the city center and green backyards.

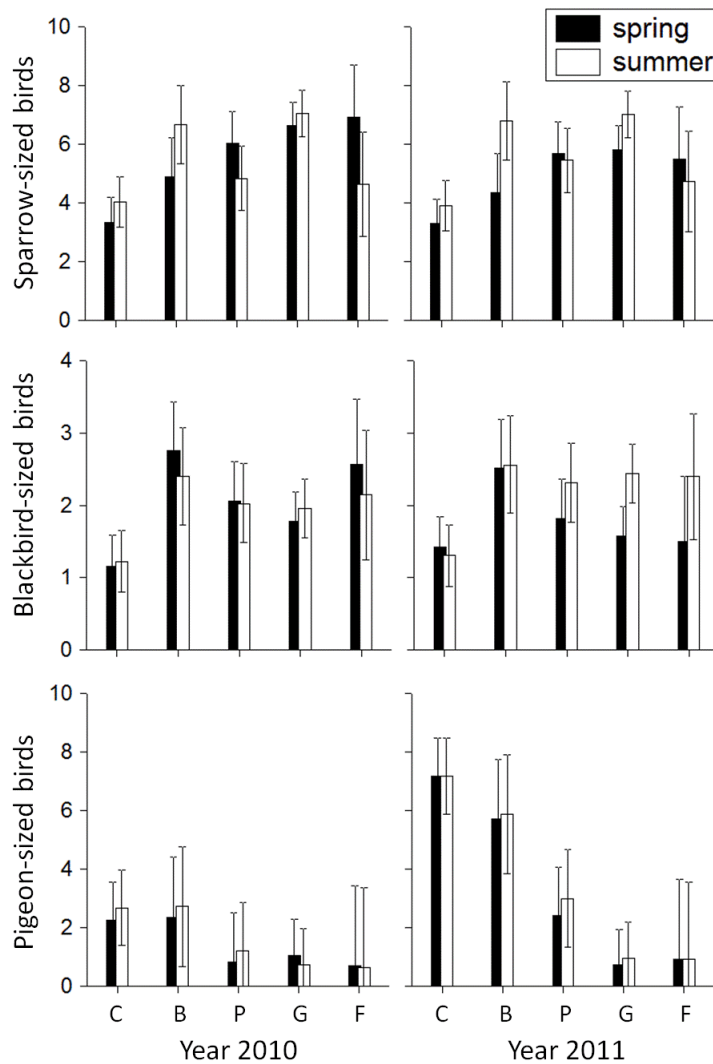


Fig. 3: Effects of habitat type (C – city center, B – green backyard, P – park, G – garden, F – forest) and season on the mean number (least-squares mean \pm 95% CI) of sparrow-sized, blackbird-sized and pigeon-sized birds counted at census points in two different years.

4. Discussion

4.1. The link between landscape composition, nest occupation and breeding success

Our results indicate a trade-off between higher nest-site availability in the center and longer distances to larger foraging grounds, making avian prey the main prey category and lowering reproduction rate. Factors such as the city size, the urban landscape composition and the historical building structure affect urban biodiversity, determining the availability of prey for raptors and thus the habitat quality. We did not find a factor discriminating between nest success and failure on the macro-habitat scale, but PC3 (high percentage of fields, low forest cover) was

connected to larger fledged brood sizes in all years, clearly favoring suburban areas in respect to breeding success.

4.2. Nest-site choice and breeding performance

The density of the Viennese kestrel population can be explained by the diverse building structure in the historical center, resulting in high nest-sites abundance, indicated by the preference for breeding in roof-openings. Breeding in close vicinity to green backyards was linked to earlier laying dates, greater clutch size, and higher hatching rates leading to significant larger fledged brood sizes. This indicates that the immediate nest surroundings influence breeding success, thus we hypothesize that kestrels hunt in the vicinity of their nests. Nonetheless, the inner-city habitat in general, with longer distances to larger green space, proved to be less productive, with smaller fledged brood sizes, than suburban areas.

A high degree of urbanization is known to be unfavorable for many passerines (e.g. Chamberlain et al., 2009; Solonen, 2001) and also for raptors, with the exception of kestrels (Sorace and Gustin 2010). Our results indicate that the historical center of Vienna offers numerous nest-sites, albeit unfavorable conditions for successful breeding. Hence, our findings alter previous results substantially by broadening the focus from breeding density and success to including habitat use versus habitat availability and the influence of landscape features and building structure on breeding parameter separately.

4.3. Brood-niche structure and conservation concern

Currently, most kestrels in Vienna breed on buildings in the center, whereas artificial nest-boxes are rare. But, kestrels are facing a diminishing number of nest-sites on inner-city buildings due to widespread renovation; a trend also documented in other cities, such as Paris, France (Malher et al. 2010) or Bardejov, Slovakia (Mikula et al. 2013).

Our detailed results on nest-site availability (random buildings) and breeding performance in different urbanized areas show that kestrels are drawn to the center by available brood-niches, but suffer lower breeding success when breeding in roof-openings than their suburban conspecifics in nest-boxes and even in open window-boxes. A nest-box program in Vienna is strongly recommended, if only to offer alternative nest-sites to those recently lost; also these boxes should be concentrated in suitable habitats, namely suburban areas, to prevent creating potential ecological traps (reviewed in Battin 2004; Kokko and Sutherland 2001; Kristan 2003; Robertson and Hutto 2006; Schlaepfer et al. 2002). The positive media coverage, which helped build the nest-site database for our study, ensured public support for the project and will no doubt facilitate any conservation related efforts in the future. Conservation efforts in cities should preserve conditions such as habitat heterogeneity, availability of food sources and suitable nest-sites in buildings, all of which benefit species of conservation concern. Kestrels are in moderate continuing decline in the European Union, categorized as SPEC 3, a Species of Europe-

an Conservation Concern (see Pople and Zoest 2004). Therefore, also urban populations ought to become the subject of conservation efforts. Early action is needed to prevent the Eurasian kestrel from following the same trend as the American kestrel (*F. sparverius*), which also inhabits its urban habitats yet is facing an alarming decline (Smallwood et al. 2009).

Comparing reproductive data from nest-boxes and natural nest-sites has shown larger clutches in nest-boxes (López et al. 2010), which is to be expected from a nest-box program. An important factor influencing breeding success may also be the size of the brood niche (Carrillo and González-Dávila 2009). Though we measured every breeding-cavity, we could not find a correlation between size and number of eggs. This is in line with studies on kestrel nest-box size and orientation, neither showing an impact on clutch size or number of fledglings (Valkama and Korpimäki 1999). It is likely that kestrels in Vienna have already adapted their clutch sizes to a less productive urban environment (smaller clutches in crow nests on inner-city facades, but not in tree broods in the SA). Comparable findings are known from northern populations, where kestrels cope with fluctuating food-conditions (three year vole cycle) by reducing the number of eggs under low prey abundance (Korpimäki and Wiehn 1998).

4.4. Diet choice and distribution of avian prey

The large home ranges of raptors can extend beyond urban boundaries (Chace and Walsh 2006), yet considering kestrels' high reproductive potential (4-6 chicks) may render long distance hunting flights inefficient, especially in a large metropolis. Thus, they rely on food sources available within the urban setting and shift from small mammals as main prey category to passerines. This was shown in kestrels' diet choice analyzed based on pellets (Sumasgutner et al. 2013) and video-monitoring. Kestrels arrive in Vienna before pair formation in March, occupying the city exclusively during breeding season. We found a significant preference of urban breeding kestrels for nesting on buildings with green backyards. The value of small urban greenspaces for birds has been shown in Mexico (Carbó-Ramírez and Zuria 2011), and may also offer a high prey density for urban raptors. Comparable, our breeding bird survey revealed higher densities of sparrow-sized birds at point-counts in yards and parks than in areas with expansive impervious surfaces.

5. Conclusion

Considering the fact that kestrels are drawn into the center due to the high availability of breeding cavities, yet breeding success being generally low and numerous nesting cavities being lost recently, we recommend planning a nest-box program for suburban areas of Vienna. Our results for fledged brood sizes and the distribution of avian prey suggest nest-boxes for urban breeding kestrels to be installed on buildings in the vicinity of larger green space. Vienna offers ample city parks and a green belt along the river Danube. Additionally, suburban areas should be of special interest, as they offer favorable hunting grounds but lack adequate nest-sites.

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6. References

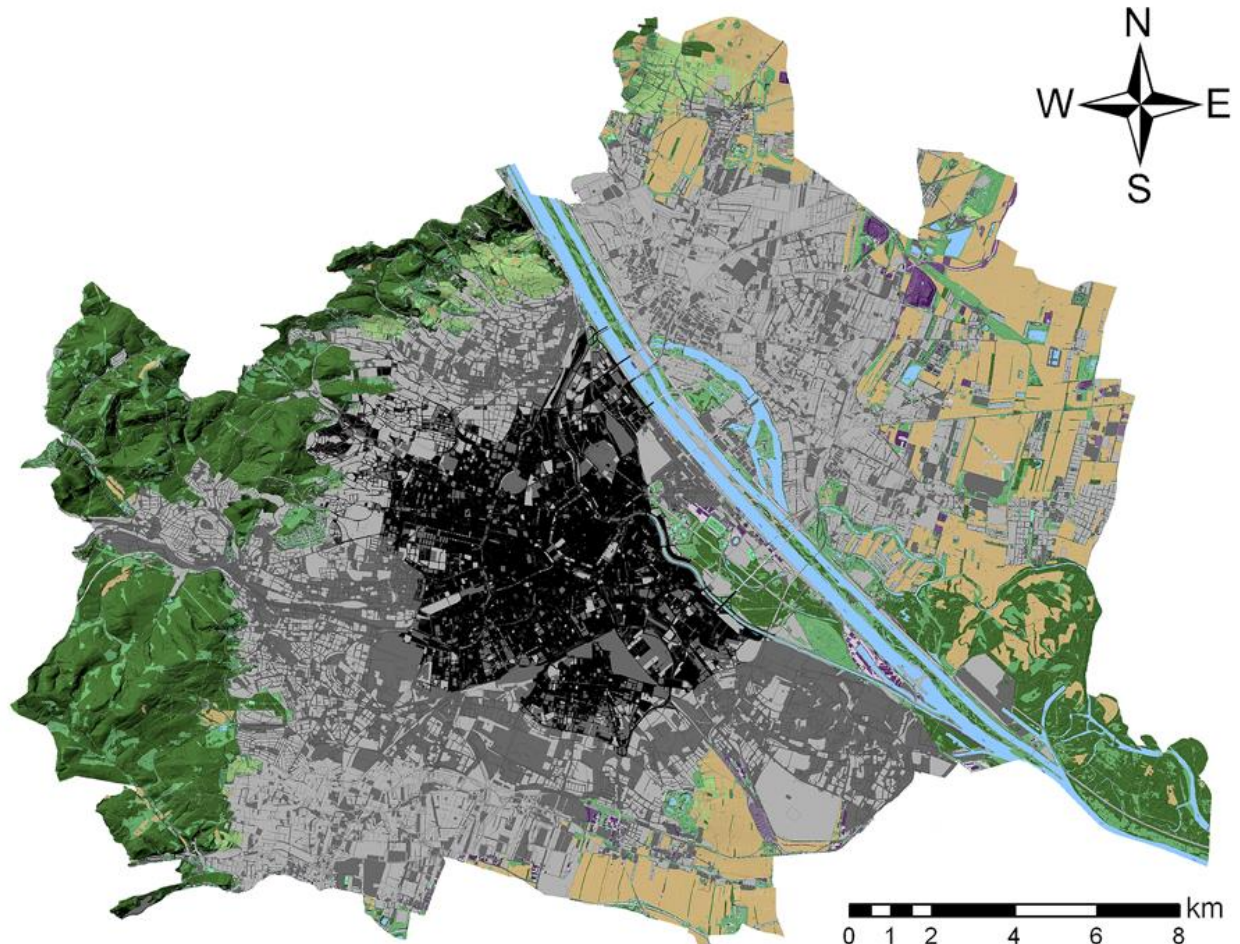
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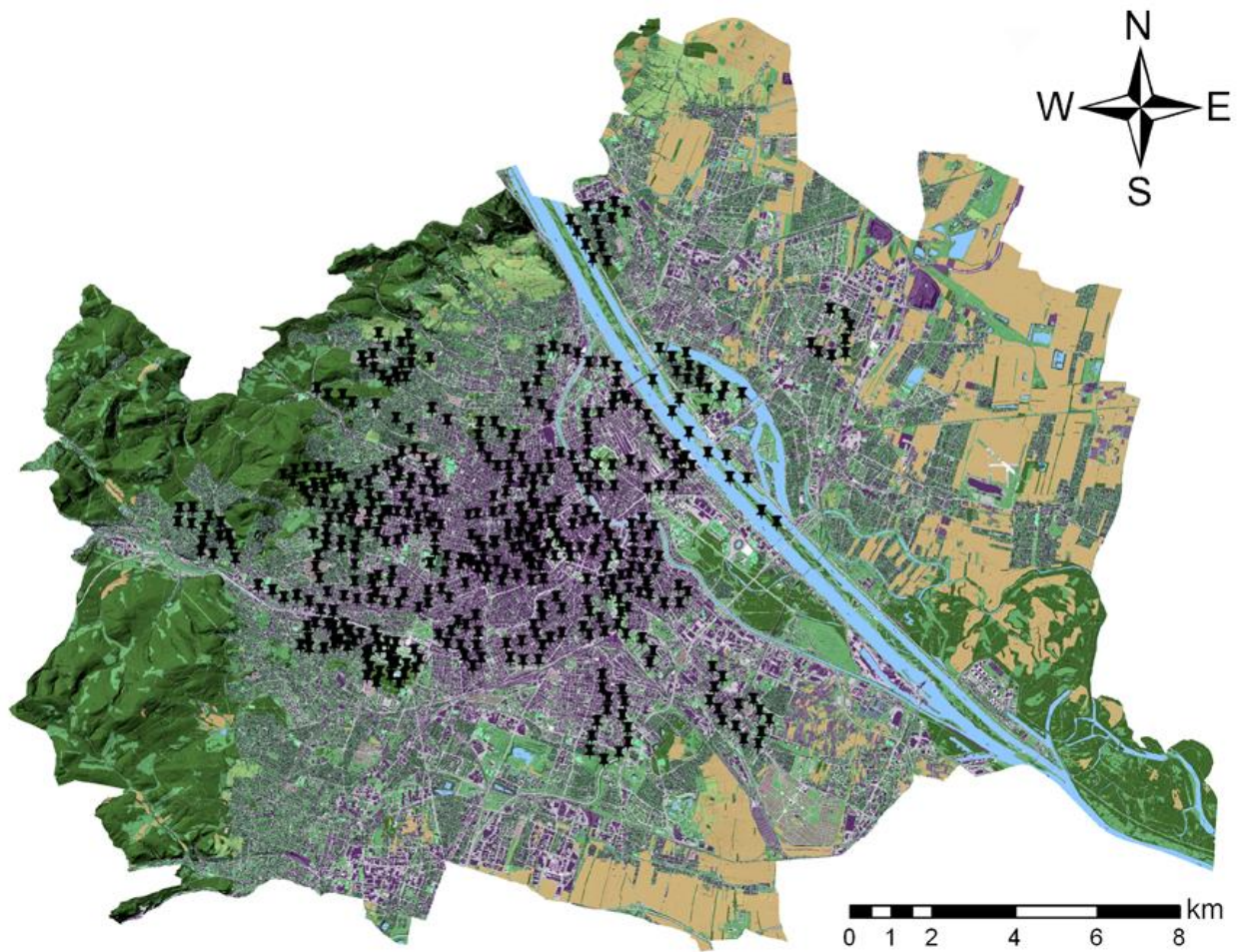
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Supplementary Material 1: The city of Vienna, 2010 in an aerial image overlaid with urban areas used for statistical analyses: city centre (black, the old town in 1775, recent impervious surfaces of > 75%), mixed zone (dark grey, parts of the old town in 1775 located at the green riverside and surrounding former cultivated landscapes, recent impervious surfaces of 45-75%) and suburban area (light grey, recent outskirts of Vienna with impervious surfaces of < 45%).



Supplementary Material 2: Bird census transects ($n=33$) in the city of Vienna in 2010 and 2011, all 5 min point-count-units are displayed in black dots.



Supplementary Material 3: Matrix of factor loadings of principal component analysis on macro-habitat variables, measured at occupied nests ($n=736$, 2010-2012) and random areas ($n=240$). Loadings are based on a correlation matrix; four factors explained 74.9% of the variance.

Variable	PC1 (47.5%)	PC2 (11.5%)	PC3 (8.3%)	PC4 (7.6%)
Building areas [%] [†]	0.38	-0.03	-0.07	0.16
Green Yards [%] [†]	0.36	0.29	0.08	-0.17
Distance [m] to green area (> 1 ha) [†]	0.37	-0.15	-0.08	-0.11
Distance [m] to green area (> 0.5 ha) [†]	0.37	-0.18	-0.05	-0.08
Distance [m] to green area (> 0.25 ha) [†]	0.36	-0.11	0.00	-0.07
Distance [m] to green area (≥ 0.01 ha) [†]	0.29	0.15	0.03	0.02
Lawns [%] [†]	-0.13	-0.65	-0.37	0.31
Fields [%] [†]	-0.25	-0.07	0.65	-0.07
Forests [%] [†]	-0.24	0.22	-0.52	0.04
Vineyard [%] [†]	-0.19	0.29	-0.36	-0.56
Cemetery [%] [†]	-0.11	-0.51	0.06	-0.68
Meadows [%] [†]	-0.26	0.06	0.13	0.22

Note:[†] Log_e transformed

Supplementary Material 4: Model selection to Table 3 in results section (dependence of fledging success on principal component scores of macro-habitat variables in glms). Models are ranked according to the Akaike Information Criterion, corrected for small sample sizes (AIC_c). The ΔAIC_c indicates AIC_c differences between a particular model and the best-fitting model that had the smallest AIC_c . Akaike weights (ω_i) indicate the contribution of each model to the average of all candidate models and K the number of parameters. Variables included and not included in a particular model are indicated with 1s and 0s, respectively. Principal component – PC, nearest-neighbor-distances – NND.

Table 3	Variables included					Model selection based on AIC_c			
	PC1	PC2	PC3	PC4	NND [†]	K	AIC_c	ΔAIC_c	ω_i
2010									
Full model	1	1	1	1	1	6	115.34	7.20	0.01
	1	1	1	1	0	5	112.48	4.34	0.05
	1	0	1	1	0	4	110.86	2.73	0.12
	1	0	1	0	0	3	108.68	0.54	0.35
Final model	0	0	1	0	0	2	108.14	0	0.46
2011									
Full model	1	1	1	1	1	6	193.89	4.64	0.06
	1	1	1	1	0	5	192.33	3.08	0.13
	0	1	1	1	0	4	191.13	1.88	0.23
Final model	0	0	1	1	0	3	189.25	0	0.59
2012									
Full model	1	1	1	1	1	6	294.52	6.15	0.03
	1	1	1	0	1	5	292.18	3.82	0.09
	1	1	1	0	0	4	290.20	1.84	0.25
Final model	1	0	1	0	0	3	288.36	0	0.63

Note: [†] Log_e transformed

Supplementary Material 5: Model selection to Table 4 in results section (dependence of breeding time and breeding parameters on building structure parameters as fixed effects in glmms; with site ID and study year as random effects). Models are ranked according to the Akaike Information Criterion (AIC_c). The ΔAIC_c indicates AIC_c differences between a particular model and the best-fitting model, Akaike weights (ω_i) indicate the contribution of each model to the average of candidate models and K the number of parameters. Variables included and not included are indicated with 1s and 0s, respectively. Laying date – cd, urban zone – uz, building type – bt, nest-type – nt, crow nest – cn, exposition – ex, façade structure – fs, roof openings – ro, other niche structures – on, presence or absence of green backyards – by, distance to the nearest open space (size categories: > 1 ha, > 0.5 ha, > 0.25 ha, ≥ 0.01 ha) – s1, s2, s3, s4 respectively.

Table 4	Variables included										Model selection based on AIC _c			
Laying date	nt	ex	ro	s2 [†]	s4 [†]						K	AIC _c	ΔAIC_c	ω_i
Full model	1	1	1	1	1						11	1185.03	5.19	0.04
	1	1	1	0	1						10	1182.96	3.12	0.11
	0	1	1	0	1						9	1180.98	1.13	0.31
Final model	0	1	0	0	1						8	1179.85	0	0.54
Clutch size	ld [†]	cn	by	s1 [†]							K	AIC _c	ΔAIC_c	ω_i
Full model	1	1	1	1							7	45.3	2.2	0.12
	1	1	0	1							6	43.83	0.74	0.25
	1	1	1	0							6	43.63	0.54	0.27
Final model	1	1	0	0							5	43.09	0	0.36
Hatching rate	ld [†]	uz	bt	nt	ro	by	s1 [†]	s2 [†]	s3 [†]	s4 [†]	K	AIC _c	ΔAIC_c	ω_i
Full model	1	1	1	0	0	1	1	1	1	0	16	167.22	20	0
	1	1	1	1	1	1	1	1	1	1	20	163.90	16.67	0
	1	1	1	1	1	1	1	1	1	0	19	161.73	14.50	0
	1	1	0	0	0	1	1	1	1	0	10	155.64	8.41	0.01
	1	1	1	0	1	1	1	1	1	0	16	155.49	8.26	0.01
	1	0	0	0	0	1	1	1	1	0	8	151.49	4.26	0.08
	1	0	0	0	0	1	1	1	0	0	7	149.27	2.04	0.24
Final model	1	0	0	0	0	1	0	0	0	0	5	147.23	0	0.66
Fledged brood size	ld [†]	uz	nt	ex	ro	on	fs	by	s1 [†]	s2 [†]	K	AIC _c	ΔAIC_c	ω_i
Full model	1	1	1	1	1	1	1	1	1	1	18	287	9.28	0.01
	1	1	1	1	1	0	1	1	1	1	17	284.85	7.13	0.02
	1	1	1	1	1	0	1	1	1	0	16	282.88	5.16	0.04
	1	1	1	1	1	0	1	1	0	0	15	280.87	3.15	0.11
	1	1	1	1	0	0	1	1	0	0	14	278.89	1.17	0.30
Final model	1	1	1	1	0	0	0	1	0	0	13	277.72	0.00	0.53

Note: [†] data presented as residuals with the study year, [†] log transformed

Supplementary Material 6: Results of glms testing for effects of land use, season and year (including all interaction terms) on the number of birds counted at census points. Glms were calculated separately for sparrow-sized, thrush-sized and pigeon-sized birds.

Effect	df	Sparrow-sized birds			Thrush-sized birds			Pigeon-sized birds		
		Mean squares	<i>F</i>	<i>P</i> -value	Mean squares	<i>F</i>	<i>P</i> -value	Mean squares	<i>F</i>	<i>P</i> -value
Constant	1	17317.31	1500.67	<0.0001	2384.48	811.17	<0.0001	3759.75	139.27	<0.0001
Land use	4	297.88	25.81	<0.0001	36.28	12.34	<0.0001	640.64	23.73	<0.0001
Season	1	10.64	0.92	0.3373	3.86	1.31	0.2524	4.49	0.17	0.6835
Year	1	9.29	0.81	0.3698	0.08	0.03	0.8711	580.16	21.49	<0.0001
Land use x Season	4	46.80	4.06	0.0029	3.31	1.13	0.3426	1.88	0.07	0.9911
Land use x Year	4	2.85	0.25	0.9115	1.14	0.39	0.8184	208.10	7.71	<0.0001
Season x Year	1	21.69	1.88	0.1708	11.38	3.87	0.0496	0.07	<0.01	0.9591
Land use x Season x year	4	2.98	0.26	0.9048	2.44	0.83	0.5068	2.09	0.08	0.9892
Error	813	11.54			2.94			27.00		

Part 1

Chapter III: Sumasgutner P, Krenn HW, Duesberg 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.



Photo: Franz Kerschbaum

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Diet specialisation and breeding success along an urban gradient: the kestrel (*Falco tinnunculus*) in Vienna, Austria

Key words: urban gradient, *Falco tinnunculus*, diet choice, pellet analysis, alternative prey, breeding success

1. Introduction

Urban areas are habitats characterised by a high degree of sealed soil and correspondingly low percentage of green space. Numerous European cities have a longstanding tradition of urban ecology research. In the area of urban zoology the avifauna is a research subject of particular interest. Previous studies focused on the abundance of different bird species and their foraging and breeding behaviour but rarely on the basis of an urban gradient, factoring in the differences between dense city centres and suburban areas. A number of bird species have adapted to live in the city by increasing their population density, by extending their diurnal rhythm and their breeding season and reducing their migratory behaviour (CHAMBERLAIN et al. 2009). The success of a species in urban areas depends highly on an appropriate food supply. Only this along with other necessary conditions like the availability of nest-sites allow for the establishment of a breeding population (WITT 2000).

Among all birds of prey the Eurasian kestrel (*Falco t. tinnunculus* Linnaeus, 1758) is the most abundant aerial predator in Vienna, Austria, with approximately 250–400 breeding pairs

(WICHMANN et al. 2009). The population density in urban areas in Europe is generally higher than those in rural areas (MEBS and SCHMIDT 2006). This may be due to the diverse structures offered in cities and a correlating abundance of prey animals. Food provided by humans in urban habitats improve adult conditions in passerine birds during the winter, leading to earlier lay dates and to higher survival rates and breeding densities (CHAMBERLAIN et al. 2009). The kestrel, however, is not found in Vienna during winter months, thus there have to be other reasons for the high breeding density. Unlike passerines, raptors need large home ranges. These may extend beyond the urban boundaries and therefore they do not need to satisfy all their ecological requirements within urban areas (CHACE and WALSH 2006). But considering the high effort required to raise numerous chicks, it may be inefficient to fly long distances to hunt. Meeting food requirements within the urban setting can constitute positive population responses in predatory birds (CHACE and WALSH 2006).

Particularly specialised bird-feeders like the goshawk (*Accipiter gentilis*), the sparrowhawk (*Accipiter nisus*) or falcon species respond well to urban landscapes because of the large bio-

mass of small birds, e.g. (NEWTON 1980, CADE et al. 1996, TELLA et al. 1996, BERRY et al. 1998, KENWARD 2006). This may also apply to kestrels. Although normally classified as a ground hunter, kestrels have been recorded preying upon birds in several cities (GALANOS 1991, PIATTELLA et al. 1999, SALVATI et al. 1999); in the centre avian prey can even serve as predominant prey category (KÜBLER et al. 2005, DÜESBERG 2012). Additionally, kestrels enrich their diet with insects (RIEGERT et al. 2009), especially in summer and early autumn, which is likely determined by its availability (KORPIMÄKI 1986, RIEGERT and FUCHS 2004) and play a decisive role in the feeding habits of juvenile kestrels (SHRUBB 1993). Since urban vegetation is of anthropogenic origin, it largely differs in structure and composition from the natural vegetation in the surrounding area (SMITH et al. 2006) as well as in between cities. Such singularities affect urban biodiversity, determining the availability of prey for raptors and therefore the habitat quality around their nest-sites. These differences in prey availability are additionally related to the degree of sealed soil, the building structure or the utilisation of pesticides in green space.

The increased preference of kestrel for hunting birds may thus be attributed to an urban gradient. The possible existence of an urban gradient concerning the foraging behaviour has so far only been investigated in Berlin through the accurate characterisation of the breeding sites in connection with prey selection (KÜBLER et al. 2005).

The 'optimal foraging theory' (STEPHEN and KREBS 1986) predicts that prey types are added to diet in order of their profitability. The longer the distance to the hunting ground, the bigger the prey must be to justify the effort. On the other hand, the 'alternative prey hypothesis' states that a predator with strong preferences for a main prey will switch to an alternative prey only when the main prey is scarce (LACK 1954).

This is true for prey that fluctuates in numbers between years, like voles (KJELLANDER and NORDSTRÖM 2003), but could also play a role in the cost and benefit calculation in urban breeding kestrels. Voles are richer in nutritional value and poorer in their carotenoid value

compared to passerine birds (GOODWIN 1980, KIRKWOOD 1991). To hunt voles, urban kestrels have to fly long distances (RIEGERT et al. 2007); therefore they may switch to prey of similar size with poorer caloric intake but occurrence in inner city districts, like passerines.

We suppose that the cost-benefit ratio (defined by nutritional value and hunting effort) shift along the urban gradient. It has to be considered that the prey abundance may not be equal to availability. For example, house mice (*Mus musculus*) and nocturnal field mice (*Apodemus* sp.) are abundant in Viennese inner-city districts (SIEBER and UIBEL 1998) but are not accessible to kestrels.

Hence we hypothesise that urban Kestrels specialise in hunting birds, as diurnal rodents are not readily available in the city centre (MITTER 2012). In this study we focus on the question of how kestrels cope with environments of varying urbanity in terms of foraging and breeding behaviour. Therefore, nest-sites along an urban gradient from the city centre to suburban areas were analysed. The urban gradient formed the essential factor, to which all other research parameters have been related.

2. Material and Methods

2.1. Study species

The Eurasian kestrel, hereafter kestrel, is with an estimated population density of 60.2–96.4 breeding pairs (bp)/100 km² (WICHMANN et al. 2009) the most abundant raptor in Vienna, Austria (415 km², 1.7 million inhabitants). This density is higher than in other European cities, e.g. 22.9–33.3 bp/100 km² in Berlin, Germany (KUPKO et al. 2000) or 40–55 bp/100 km² in Paris, France (MALHER et al. 2010), and higher than in rural areas in Austria with 8–30 bp/100 km² (GAMAUF 1991) and Europe (MEBS and SCHMIDT 2006).

In general, kestrels use diverse hunting strategies like perched-hunting, flight-hunting, including hover-hunting, and quite seldom, hunting for invertebrates by foot, but over all kestrels are classified as ground hunters (VILLAGE 1990). Kestrels return to Vienna before pair formation at the end of March and remain at their breeding sites until August.

2.2. Study area

To represent urbanisation as an environmental feature rather than a geographical one, soil sealing was chosen as criteria for defining urbanisation. To study feeding ecology of kestrels along an urban habitat gradient, the municipal area of Vienna was divided into three urban zones (fig. 1): 1 – the city centre (CC) with 81 to 100 % soil sealing, 2 – the mixed zone (MZ) with 51 to 80 % soil sealing, and 3 – the suburban area (SA) with less than 50 % soil sealing. Unsealed soil (< 1 %) was defined as rural and excluded from this investigation. Disregarding the surrounding mostly forested areas, the urban study area covered 243 km². The soil sealing factor was calculated based on georeferenced aerial images and a land allocation map in ArcGIS 10 (by ESRI ©). The or-

thophoto (resolution 15 cm) and the map (scale 1:7 500) were provided by the Environmental Protection Bureau of Vienna (MA 22). During the two year study period (2010–2011) we build a data-base with 379 recent nest-sites within the urban study area (243 km²), between 66 % ($n = 251$ nests) and 78 % ($n = 297$) of which have been occupied each year.

2.3. Breeding parameters

In Vienna, kestrels predominantly breed in building cavities (68.5 %, $n = 251$) where they especially use roof openings (40.9 %). Abandoned nests on trees play a minor role (17.5 %). Currently there is no organised nest-box program in Vienna; hence kestrels rarely use nest-boxes (5.6 %). Between 2010 and 2011 occup-

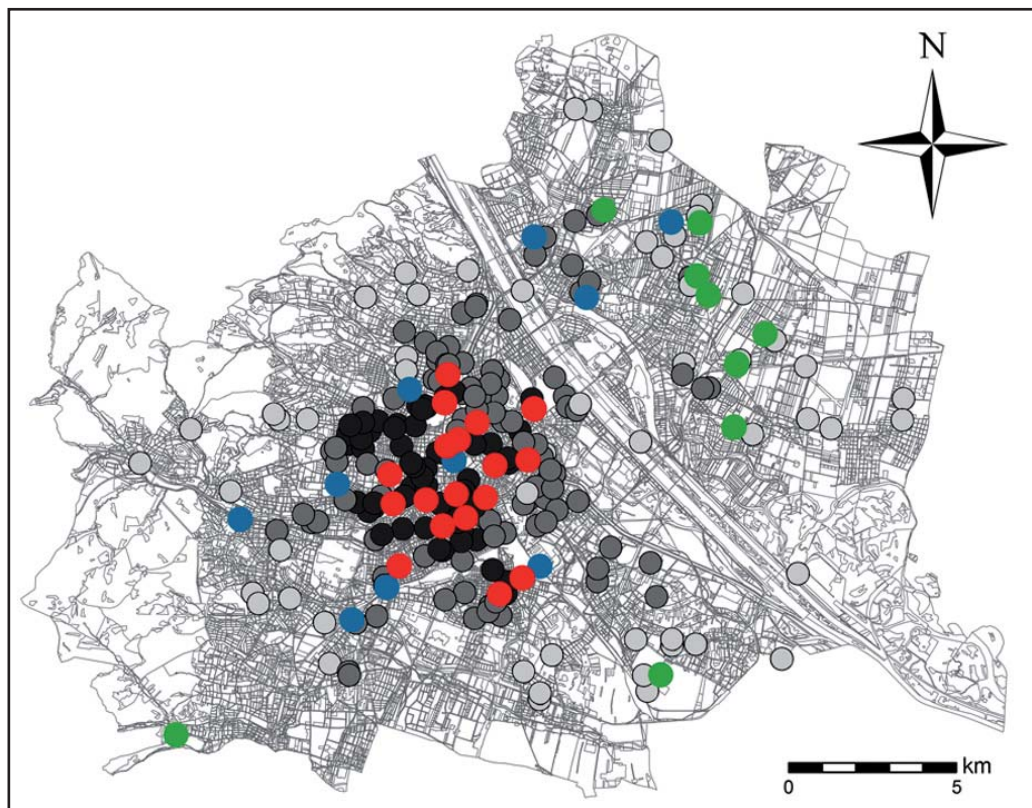


Fig. 1 Urban gradient and nest-sites of *Falco tinnunculus* in Vienna in 2010 ($n = 251$) according to percentage of sealed soil: city centre (black, 81–100 % soil sealing, $n = 81$), mixed zone (dark grey, 51–80 % soil sealing, $n = 109$) and suburban area (light grey, 1–50 % soil sealing, $n = 61$); white – unsealed soil, defined as rural and excluded from the study. Nest-sites used for pellet analysis are coloured in red (CC), blue (MZ) and green (SA).

ied nests which were accessible via the attic or by climbing were monitored 4–6 times during the breeding season to determine (1) the egg-laying date, (2) clutch size, (3) the number of hatched offspring and (4) the number of fledged young. A total number of 88 kestrel broods were examined (36 nest-sites in 2010 and 52 in 2011). Egg-laying date was either specified by direct observation or calculated based on the age of the nestlings. During monitoring, the nestlings were measured, weighed and banded (ring from Ringing-Centre in Radolfzell, Germany). An additionally electronic-coded PIT-ring was coloured according to the respective zone and labeled with contact information to facilitate the reporting of findings. Morphological key characters were measured at culmen, tail, wing, tarsus, claws and feet (ECK et al. 2011) for age determination (KOSTRZEWA and KOSTRZEWA 1993).

2.4. Pellet collection and diet analysis

During both breeding seasons pellets and other prey remains were collected at the nests. Thus, no distinction was made between the pellets of the nestlings and those of the adults. At each visit we took 1/3 of the nest content. In total we collected 637 pellets and prey remains at 37 different nest-sites to analyse feeding habits of kestrels (CC: $n = 18$ nests, 288 pellets, MZ: $n = 10$ nests, 206 pellets, SA: $n = 9$ nests, 143 pellets, fig. 1). The pellets were dissected; prey remains were classified as ‘mammals’, ‘birds’, ‘reptiles’ or ‘insects’. We identified prey items to species level if possible with the aid of reference collections (at the Museum of Natural History Vienna). Pellets were analysed dry. We assessed the minimum number of each prey category per pellet (highest number of different jaws, upper or lower mandibles, skulls, pairs of incisors in small mammals; upper or lower beaks, left or right feet, plugged feathers in birds; pairs of mandibles, wings or tarsi, ovipositors for insects), whilst fur or feathers occurring on their own were considered as coming from one individual. Prey constancy (C) was calculated as the percentage of nests in which the prey category was found. Conversion from prey items to prey weights is particularly difficult in smaller raptors, because

we have to assume that larger prey species are only partially consumed (ARROYO 1997). However, when combining prey categories as different as insects and pigeons, an estimate of their contribution in biomass is needed to evaluate the importance of the different prey categories in the diet. Thus, diet data are presented both as the percentage of identified prey and their estimated biomass [g]. For the latter, we used the biomass of prey item according to Glutz von Blotzheim and Bauer (1980) or following estimated average biomass for each prey class: 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 insects. Data were not normally distributed; hence we performed Kruskal-Wallis χ^2 as nonparametric test.

For the analysis of diet composition, prey frequency in the pellets was defined by the number of individuals found rather than the number of pellets which contained that prey category since more than one individual per pellet appeared regularly in some categories (such as mammals or insects) but rarely in others (such as birds). We calculated indices of diet diversity and diet breadth for each zone. Diet diversity (H) was determined using the Shannon-Wiener diversity index with the equation $H = -\sum p_i \log p_i$, where $p_i = X_i/X$; X_i = number of prey items taken from class i and X = total number of prey items. Diet breadth (B) was calculated according to Levins (1968), as $B = 1/\sum p_i^2$, where p_i is the proportion of the diet contributed by prey type i . Levin's index tends to weight in favour of abundant prey types, and was preferred over the Shannon index, which tends to give more weight to rare groups (KREBS 2004). To analyse the relation between diet diversity and breeding parameters (clutch-size and number of fledglings) we used logistic regressions. All statistical analyses were carried out in Statistica 7.1 (Statsoft, 2005).

3. Results

The nest-site monitoring in 2010 resulted in 251 occupied nest-sites. In 2011 we observed 297 breeding pairs within the same study area. This amounts to a breeding pair density of 103.3 – 122.2 bp/100 km² in urbanised areas of Vienna (243 km²).

3.1. Diet choice

There was no significant difference in proportion of main prey categories among years (table 1, Kruskal-Wallis χ^2 mammals: $\chi^2_{df=1} = 1.14$, $P = 0.29$, birds: $\chi^2_{df=1} = 0.51$, $P = 0.48$, reptiles: $\chi^2_{df=1} = 0.24$, $P = 0.62$ and insects: $\chi^2_{df=1} = 1.52$, $P = 0.22$). Therefore we pooled the data for further analysis. Pellet analysis based on percentage of biomass of prey items showed significant differences among urban zones (fig. 2): in the city centre pellets consisted of 48.5 % mammals, 39 % birds, 3.5 % reptiles and 9 % insects. In the MZ, pellets consisted of 56.6 % mammals, 29.8 % birds, 1.5 % insects and 12.1 % reptiles. The compared pellets in SA showed 79.6 % mammals, 12.2 % birds, 4.2 % insects and 4.0 % reptiles. The ratio of mammals to birds as main prey categories differed significantly among the zones (mammals: Kruskal-Wallis $\chi^2_{df=2} = 7.54$, $P = 0.02$ and birds: $\chi^2_{df=2} = 7.24$, $P = 0.03$). Reptiles were found by trend more often in the mixed zone (Kruskal-Wallis $\chi^2_{df=2} = 5.67$, $P = 0.06$) and insects were equally used (Kruskal-Wallis $\chi^2_{df=2} = 0.61$, $P = 0.74$). Mammals were constantly present in pellets occurring in 82.1 % of pellets analysed. Birds ($C = 47.7\%$) and insects ($C = 48.2\%$) were commonly used, whereas reptiles were rarely consumed ($C = 23.4\%$).

Diet diversity based on composition of kestrel pellets was very low in the suburban area (fig. 2) compared to the inner-city districts. This change in diet diversity was associated with the progressive inclusion of more avian prey in

the diet towards the centre, and an increasing proportion of mammals towards the suburban areas (table 1). Diet breadth (Levin's index) differed significantly along the urban gradient ($\chi^2_2 = 8.34$, $p = 0.0155$), as well as the Shannon-Wiener diversity index ($\chi^2_2 = 9.93$, $p = 0.007$).

We identified 11 species of small mammals, mostly rodents, 19 species of birds, mostly passerines and 3 species of reptiles in pellets analysed (table 2). We could not identify all pellet contents to the species level, but 70.4 % of identified small mammals were *Microtus arvalis* voles (sub sample size: $n = 152$).

The most common avian prey type were the tit (*Parus major*, *Cyanistes caeruleus*, *Periparus* sp. $n = 29$) and the sparrow (*Passer domesticus*, *P. montanus* $n = 19$). We identified 31 feral pigeons (*Columba livia*), which were all collected at two different nest-sites occupied in both years (one building cavity in the MZ and one window box in the SA). The most common arthropods were beetles, with at least 26 different taxa (table 3), followed by grasshoppers, where we found 9 different taxa.

We could identify anthropogenic food items at three different nest-sites. In the suburban area we collected a bacon rind in a nest-box and several sausage casings in a window-box. Both 'owners' of the kestrels brood ensured that they have not fed the kestrels directly with those food items. Additionally we found cutlet bones in a building cavity in the city centre, a breeding site which is normally not accessible for humans.

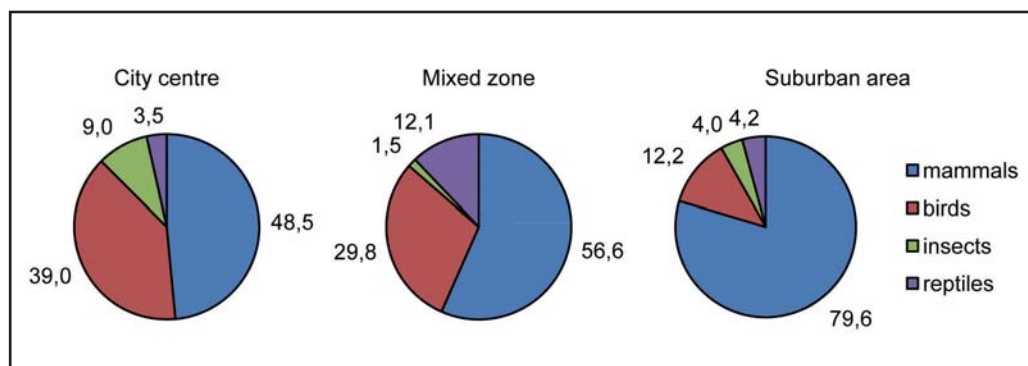


Fig. 2 Proportions of main prey categories in percent (based on calculated biomass of prey items) of kestrel pellets from three urban zones in Vienna: city centre ($n = 18$ nest-sites), mixed zone ($n = 10$ nest-sites) and suburban area ($n = 9$ nest-sites).

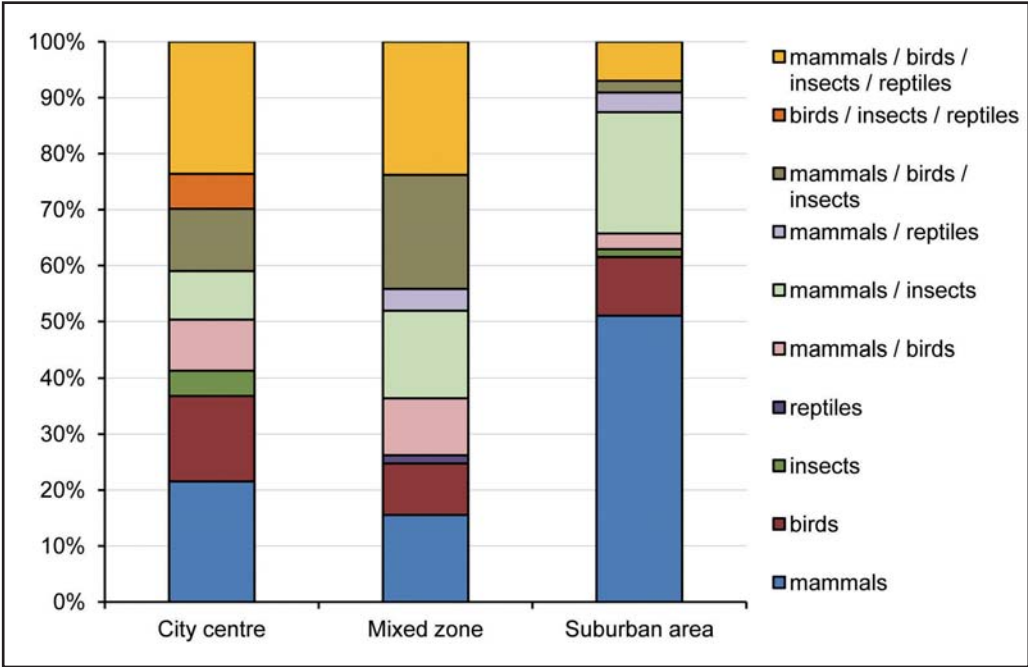


Fig. 3 Composition of kestrel pellets from three urban zones in Vienna (n = 637 pellets).

Table 1 Diet of kestrels in Vienna along the urban gradient for each study year; presented as proportion of main prey categories in percent (based on calculated biomass of prey items) and prey diversity indexes.

Zone/year	Proportion [%] of main prey categories				Prey diversity	
	Mammals	Birds	Reptiles	Insects	Shannon-Wiener Index	Levin's Index
City centre					0.27	4.02
2010	56.37	36.91	4.60	2.13	0.28	3.84
2011	37.33	47.24	2.47	12.95	0.25	4.40
Mixed zone					0.26	3.10
2010	46.66	40.61	12.00	0.73	0.21	2.77
2011	51.48	39.81	5.08	3.63	0.31	3.44
Suburban area					0.07	1.44
2010	78.87	12.52	2.17	6.44	0.03	1.22
2011	80.63	11.87	6.81	0.69	0.09	1.49

Table 2 Identified prey items found in kestrel pellets in main prey categories in Vienna.

Prey category	n	Prey species	
Mammals n = min. 573 ind. (523 pellets)	152	Common vole	<i>Microtus arvalis</i>
	28	Field mouse	<i>Apodemus</i> spp.
	10	Shrew	<i>Sorex</i> spp., <i>Crocidura suaveolens</i>
	5	House mouse	<i>Mus musculus</i>
	4	Bank vole	<i>Myodes glareolus</i>
	3	Harvest mouse	<i>Micromys minutus</i>
	2	European mole	<i>Talpa europea</i>
	1	Least weasel	<i>Mustela nivalis</i>
	1	Mouse-eared bat	<i>Myotis myotis</i>
	1	Souslik	<i>Citellus citellus</i>
Birds n = min. 345 ind. (304 pellets)	31	Feral pigeon	<i>Columba livia</i>
	29	Tit	<i>Parus major</i> , <i>Cyanistes caeruleus</i> , <i>Periparus</i> spp.
	19	Sparrow	<i>Passer domesticus</i> , <i>P. montanus</i>
	16	Greenfinch	<i>Carduelis chloris</i>
	16	Thrush	<i>Turdus merula</i> , <i>T. philomelos</i>
	12	Common swift	<i>Apus apus</i>
	5	Starling	<i>Sturnus vulgaris</i>
	5	Black redstart	<i>Phoenicurus ochruros</i>
	4	Collared dove	<i>Streptopelia decaocto</i>
	3	Eurasian kestrel	<i>Falco tinnunculus</i>
	2	Sky lark	<i>Alauda arvensis</i>
	2	Chaffinch	<i>Fringilla coelebs</i>
	1	Goldfinch	<i>Carduelis carduelis</i>
	1	Robin	<i>Erithacus rubecula</i>
	1	Middle spotted woodpecker	<i>Dendrocopos medius</i>
Reptiles (149 pellets)	22	Sand lizard	<i>Lacerta agilis</i>
	5	Slow worm	<i>Anguis fragilis</i>
	2	Grass snake	<i>Natrix natrix</i>

3.2. Breeding success and diet diversity

In total, breeding success of the controlled nests in both years decreased with increasing soil sealing factor (table 4). In 2010 the loss rate of 41.2 % between hatching rate and fledge rate was high in the CC compared to 9.1 % in the SA. All breeding parameters except the egg-laying date showed significant differences among zones. In 2011, only the clutch size differed significantly. Additionally, kestrels in the CC started egg laying significantly later than

those in SA. Between years, the clutch size and the fledging rate differed significantly, being lower in 2010 than in 2011 (Kruskal-Wallis $\chi^2_{(1,88)} = 5.16$, $P = 0.0231$ and $\chi^2_{(1,88)} = 4.7$, $P = 0.0301$).

If we analyse the influence of prey consumed by kestrels and their breeding success, we found by trend smaller clutches with increasing diet breadth from the periphery toward the centre (Levin's index: $R = 0.31$, $R^2 = 0.09$, $F_{(1,28)} = 2.99$, $P = 0.0943$, $SE = 1.26$), along with a

Table 3 Arthropods as prey of kestrels in three urban zones in Vienna; chitin parts occurred in 307 pellets, 414 prey items could be identified at least to insect order level and were listed according to their numbers.

Arthropods	Family	Prey species	Min number of individuals			Total
			City centre	Mixed zone	Suburban area	
Coleoptera	Buprestidae	Indet.	1	-	-	1
	Carabidae	<i>Calosoma</i> sp.	-	4	1	5
		<i>Carabus</i> sp.	20	6	-	26
		indet.	10	15	3	28
	Cerambycidae	indet.	-	2	3	5
	Coccinellidae	indet.	1	1	-	2
	Curculionidae	<i>Phyllobius</i> sp.	1	-	-	1
		indet.	8	5	2	15
	Dytiscidae	indet.	1	2	-	3
	Elateridae	indet.	2	-	1	3
	Geotrupidae	<i>Geotrupes</i> sp.	2	-	-	2
		indet.	2	7	-	9
	Histeridae	indet.	10	-	-	10
	Lucanidae	indet.	1	1	2	4
	Scarabaeidae	<i>Cetonia aurata</i>	35	33	10	78
		<i>Oxythyrea</i> sp.	-	1	-	1
		<i>Potosia</i> sp.	-	2	-	2
		<i>Melolontha</i> sp.	1	-	-	1
		indet.	8	-	1	9
	Silphidae	indet.	1	1	-	2
	Staphylinidae	indet.	1	-	-	1
	indet.		48	57	11	116
Orthoptera	Gryllidae	<i>Gryllus campestris</i>	-	-	1	1
	Gryllotalpidae	<i>Gryllotalpa gryllotalpa</i>	-	2	3	5
	Phaneropterinae	indet.	-	2	-	2
	Tettigoniidae	indet.	15	5	-	20
		indet.	4	2	6	12
Hymenoptera	Apidae		-	1	-	1
	Crabronidae	<i>Philanthus</i> sp.	1	1	-	2
	Formicidae	indet.	21	3	12	36
		indet.	3	2	-	5
Heteroptera	indet.		3	1	-	4
Diptera	indet.		1	-	-	1
Odonata	indet.		1	-	-	1

Table 4 Breeding parameters of kestrels 2010-2011 in the city of Vienna ($n = 88$ nest-sites in total) along the urban gradient. Significant results are shown in bold.

	City centre	Mixed zone	Suburban area	Kruskal-Wallis χ^2	P-value
2010 ($n = 36$)					
laying date	May 4 \pm 6.3 days	May 3 \pm 11.9 days	Mai 1 \pm 17.6 days	0.13	0.9387
clutch size	2.52 \pm 2.06	4.58 \pm 1.73	5.00 \pm 1.41	8.53	0.0140
hatched	1.74 \pm 1.94	3.58 \pm 1.78	4.40 \pm 1.14	10.00	0.0067
fledged	1.00 \pm 1.33	1.58 \pm 1.31	4.00 \pm 1.22	11.14	0.0038
2011 ($n = 52$)					
laying date	May 4 \pm 14.4 days	May 3 \pm 15.1 days	April 19 \pm 7.2 days	6.18	0.0454
clutch size	3.88 \pm 1.86	4.46 \pm 1.48	5.75 \pm 1.16	7.70	0.0213
hatched	2.38 \pm 2.42	3.57 \pm 1.89	4.25 \pm 2.71	4.82	0.0900
fledged	1.81 \pm 1.94	2.61 \pm 1.79	3.50 \pm 2.39	3.88	0.1437

lower fledging rate ($R = 0.29$, $R^2 = 0.09$, $F_{(1,28)} = 2.53$, $P = 0.1231$, $SE = 1.75$). This results could not be repeated using Shannon-Wiener index (clutch size: $R = 0.05$, $R^2 = 0.0026$, $F_{(1,28)} = 0.07$, $P = 0.7897$, $SE = 1.33$, fledged young: $R = 0.21$, $R^2 = 0.04$, $F_{(1,28)} = 1.3$, $P = 0.2641$, $SE = 1.78$).

4. Discussion

4.1. Diet specialisation and breeding success

The large home ranges of raptors can extend beyond urban boundaries (CHACE and WALSH 2006), but the increasing proportion of alternative prey from the periphery to the centre occurring in pellets indicates that kestrels prefer hunting in the surrounding areas in spite of flying long distances to rural areas. Thus they rely on food sources available within the urban setting and shift from small mammals as the main prey category to passerines. The kestrel's diet in the city centre and mixed zone was very diverse and indicated that urban kestrels are generalists whereas their suburban and rural counterparts are specialised in hunting voles.

In this study, the annual differences in proportion of main prey categories based on the biomass of prey items (table 1) were non-significant; nonetheless the proportion of mammal and avian prey differed in the city centre between 2010 and 2011. Variation between years was probably a result of differences in availability, caused mainly by varying weather conditions. The

breeding season of 2010 was characterised by adverse cool and rainy weather, especially in May, which is the most sensitive time for small hatchlings. In 2011 a warm and dry May led to a higher breeding success. This may also explain the significant differences in kestrel's breeding success between years (table 4). Also, the lower proportion of avian prey in the CC in 2010 could be linked to general adverse weather negatively effecting breeding birds, thus avian prey was not as available in 2010 as in 2011. This difference was more visible in the centre where birds as alternative prey were especially important (fig. 1, 2).

It has to be considered that the type of prey does not only depend on the hunting site, but also on the hunting attitude of the individual bird. This was shown in the bias for feral pigeons as prey for urban kestrels (table 2). Although they represent the most identified avian prey item ($n = 31$ individuals), it has to be noted that pigeons were only found at two different nest-sites. Catching birds during flight is noteworthy accomplishment for kestrels, because their anatomy with strong legs and short digits characterises them as being adapted to catch prey on the ground (VILLAGE 1990), but it seems impossible for large avian prey like pigeons or very fast species like Swifts (*Apus apus*). We observed two hunting techniques for pigeons: 1. Female kestrels used very narrow backyards where pigeons were unable to escape and try to take-off vertically ($n = 2$ direct observations in 2010 and

2011). The raptor came from above and used its own weight to smash the pigeon to the ground. The prey was just partly transported to the nest-site. 2. A male kestrel (in 2010) hunted inside an attic and caught a very weak pigeon crouching on the ground. We never observed kestrels catching Swifts in flight, only directly in their nest by holding onto the wall and grabbing inside the nest, but we have three records of bats being caught in twilight in flight in 2012 (observed by the authors P.S., H.K. and H. Frötscher pers. comm.).

We could not find a significant influence of diet breadth (Levin's index) on breeding success, but a tendency for smaller clutches and lower fledging rate with progressive inclusion of alternative, mostly avian prey in the diet towards the centre. As Levin's index (B) tends to weight in favour of abundant prey types, we consider our results based on B as more robust than those based on Shannon-Wiener diversity index. The detected trend clearly needs further investigations of diet specialisation and nestling's body condition, as we consider starvation as main factor lowering breeding success in the city centre.

4.2. Insects in the diet of urban kestrels

The rose chafer (*Cetonia aurata*), the most commonly caught beetle species, occurs frequently during the breeding season of kestrels. The occurrence of Dytiscidae in the pellets was remarkable, as it raises the question how kestrels do catch these mainly nocturnal and aquatic beetles. KÜBLER et al. (2005) suggested for Berlin that the water beetles fly at night to floodlights, for example on churches and power plants, where they are subsequently picked by the kestrels during the daytime. This could also be true for Vienna although we have no direct observation of kestrels using this technique. We have one observation of a male kestrel catching moths under artificial light conditions around a church (P.S. August 2010), therefore it seems also possible that they hunt other nocturnal arthropods in street lights (SACHSLEHNER 1996). Very small insects (e.g. ants, table 3) appeared occasionally and only in pellets otherwise including feathers, so we assume they were pre-

sent in the crops of the prey rather than being taken by the kestrels themselves. We suggest the same for seeds found inside pellets.

Clearly, arthropods have a lower nutritional value than rodents or passerines. The relatively high percentage of insects in kestrel's prey during breeding season ($C = 48.2\%$) nevertheless raises the question of their value. Although it is known that kestrels enrich their diet with insects (KORPIMÄKI 1985, RIEGERT and FUCHS 2004, RIEGERT et al. 2009), they usually use insects mainly to feed themselves, as it doesn't seem very efficient to bring such small items to the nest. Only if larger prey were more challenging to catch, would it make sense to deliver even insects to the hungry chicks. Differences in food composition in between nests with a higher feeding frequency of insects have been shown in Poland (BORATYNSKI and KASPRZYK 2005) and were linked to a higher habitat heterogeneity. In Vienna, higher feeding rates in the center than in the periphery were detected via video-monitoring (DÜESBERG 2012). These findings confirm that relatively high nestling feeding rates may reflect the low quality of available food rather than the abundance of food in the environment (MÄGI et al. 2009).

On the other hand, it is known that raptor nestlings fed only with mice are strongly carotenoid limited (STERNALSKI et al. 2010) compared to those targeting more alternative prey (birds, insects). We detected a relatively high proportion of insects in urban kestrels' diet (with the highest value of 12.95 % in the CC in 2011, where we found numerous pellets consisting exclusively of chitin at six nest-sites, which never occurred in other study zones). Carotenoids serve important health-related physiological functions (CHEW and PARK 2004), but see also COSTANTINI and MÖLLER (2008). As vertebrates cannot synthesise these pigments *de novo*, they have to acquire them from their diet which might be limited by food resource through environment (GOODWIN 1980, OLSON and OWENS 1998). In adult kestrels the yellow-orange integument colouration is strongly associated with diet (CASAGRANDE et al. 2006). A significant association with health has been shown in American kestrels (BORTOLOTTI et al. 2000). Voles are energy rich but contain low carotenoid concentration, whereas birds and mainly insects

are carotenoid rich (GOODWIN 1980). In urban kestrels, carotenoid poor resources (voles, mice and shrews) are potentially traded for carotenoid rich resources (birds, insect). The skin colouration in juvenile kestrels has so far only been investigated by CASAGRANDE et al. (2007), results of whose were consistent with the hypothesis that there is a physiological constraint on these pigments, as well as an environmental limitation. However, further investigations are required to clarify a potential effect of insects as carotenoid source in nestlings' diet.

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Summary

The diet of Eurasian kestrels (*Falco tinnunculus*) was studied along an urban habitat gradient in Vienna, Austria, using pellets and prey remains collected during breeding season (2010–2011). In the urban study area of Vienna (243 km²), 103.3–122.2 breeding pairs/100 km² constitute the highest known population density documented in a non-colonial breeding kestrel population. In the urban setting, kestrels preferentially nest in building-cavities (68.5 %). There was no difference in proportion of main prey categories (mammals, birds, reptiles and insects) within years but significant differences between three urban zones, defined by increasing soil-sealing from the periphery to the

centre. Diet breadth (Levin's index) was very low in the suburban area compared to inner-city districts. This change in diet diversity was associated with the progressive inclusion of more avian prey and insects towards the centre and an increasing proportion of mammals towards the suburban areas. This indicates that urban kestrels are generalists whereas their suburban and rural counterparts are specialised in voles. The large home ranges of raptors can extend beyond urban boundaries, but the high proportion of alternative prey in pellets collected in the centre confirms that kestrels prefer hunting in the surrounding areas of their nest-sites in spite of flying long distances to rural areas. Thus they rely on food sources available within the urban setting and shift from small mammals as main prey to passerines. Additionally, breeding success decreased with increasing soil sealing factor, which could indicate an insufficient food supply. Analysing the influence of prey consumed and kestrels' breeding success, we found by trend smaller clutches and a lower fledging rate with increasing diet breadth from the periphery toward the centre.

Zusammenfassung

Der Turmfalke (*Falco tinnunculus*) in Wien, Österreich: Nahrung und Bruterfolg entlang eines Urbangradienten

Die Ernährung des Turmfalken (*Falco tinnunculus*) wurde entlang eines Urbangradienten in der Großstadt Wien, Österreich untersucht. Die Studie basiert auf Gewöllen und Rupfungen, die während der Brutsaisonsen 2010–2011 gesammelt wurden. Die städtische Turmfalkenpopulation von Wien (243 km²) ist mit 103,3–122,2 Brutpaaren/100 km² die höchste bisher dokumentierte Dichte einer solitär brütenden Population in Mitteleuropa. In der Innenstadt brüten Turmfalken bevorzugt in Gebäudenischen (68,5 %). Zwischen den beiden Untersuchungsjahren ergaben sich keine Unterschiede im Verhältnis der Hauptbeutekategorien (Säugetiere, Vögel, Reptilien und Insekten), jedoch signifikante Unterschiede zwischen drei über den Flächenversiegelungsgrad definierten städtischen Zonen. Die Beutediversität (Levin-Index) war im suburbanen Raum deutlich ge-

ringer als in innerstädtischen Bereichen. Diese Unterschiede in der Ernährung kamen durch einen erhöhten Anteil an Vogelbeute und Insekten in Richtung Stadtzentrum, und umgekehrt einen erhöhten Anteil an Kleinsäugetern als Hauptbeute in Richtung Peripherie zustande. Dies deutet darauf hin, dass städtischen Turmfalken Generalisten sind, während ihre ländlichen Artgenossen auf Wühlmäuse spezialisiert sind. Grundsätzlich besitzen Greifvögel recht ausgedehnte Jagdgebiete, die auch über die Grenzen einer Großstadt hinausgehen können. Der erhöhte Anteil an alternativer Beute im Stadtzentrum deutet jedoch darauf hin, dass Turmfalken bevorzugt in unmittelbarer Umgebung zum Nistplatz jagen. Demnach hängt der Bruterfolg auch von der Beuteverfügbarkeit im innerstädtischen Raum ab, was sie dazu veranlasst von Kleinsäugetern als Hauptbeutekategorie auf Kleinvögel umzusteigen. Zusätzlich verringert sich der Bruterfolg mit zunehmender Flächenversiegelung, was auf ein geringeres Beuteangebot im Stadtzentrum schließen lässt. Die Verschneidung der Nahrungsnutzung mit dem Bruterfolg ergab kleinere Gelege und niedrigere Ausflugeraten mit zunehmender Beutediversität von der Peripherie in Richtung Stadtzentrum.

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Part 2

Chapter IV: Sumasgutner P, Rubin I, Gamauf A (2014) Collecting blood samples in Eurasian Kestrels (*Falco tinnunculus*) (Aves: Falconidae) via blood-sucking bugs (Insecta: Hemiptera: Reduviidae) and their use in genetics and leucocyte profiles. — Annalen des Naturhistorischen Museums Wien, B 116:247-257.



Photo: Verena Popp-Hackner

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Collecting blood samples in Eurasian Kestrels (*Falco tinnunculus*) (Aves: Falconidae) via blood-sucking bugs (Insecta: Hemiptera: Reduviidae) and their use in genetics and leucocyte profiles

P. Sumasgutner*, I. Rubin**, A. Gamauf**

Abstract

We modified the non-invasive technique to bleed incubating birds via the blood-sucking bug *Dipetalogaster maximus* in an artificial egg for an urban breeding raptor, the Eurasian kestrel (*Falco tinnunculus*) in Vienna, Austria, in 2012. We evaluated the use of the technique for the purpose of: (1) identification of the breeding bird, (b) microsatellite analysis for paternity tests, (3) the count of blood parasites and (4) leucocyte profiles based on blood smears. We can conclude that the method is useful for identification of individuals, microsatellite analyses and blood parasite counts, as long as the bug-egg is retrieved after not later than 4 hours from the kestrel clutch and needs further evaluation for leucocyte profiles.

Key words: *Falco tinnunculus*, blood screening, artificial egg, blood-sucking bug, *Dipetalogaster maximus*, non-invasive bleeding.

Zusammenfassung

In dieser Arbeit wird eine nicht-invasive Methode zur Blutabnahme bei brütenden Vögeln über die Raubwanze *Dipetalogaster maximus* modifiziert. Dazu wurden 2012 in den zu untersuchenden Nestern der in Wien brütenden Turmfalken (*Falco tinnunculus*) künstliche Eier mit *D. maximus* Larven platziert. Diese Methode zur Blutabnahme ohne Störung des Brutgeschehens diente (1) der Identifizierung der Brutvögel, (2) der Mikrosatellitenanalyse für Vaterschaftstests, (3) dem Erfassen von Blutparasiten und (4) und der Erstellung eines Leukozytenprofils mittels Blutausrichen. Zusammenfassend kann gesagt werden, dass diese Methode für die Identifizierung von Individuen, zur Mikrosatellitenanalyse und für das Auszählen von Blutparasiten gut geeignet ist, vorausgesetzt die Raubwanze ist nicht länger als 4 Stunden im Turmfalken-gelege. Die Untersuchung von Leukozytenprofilen muss im Detail noch ausgetestet werden.

Introduction

For many endocrinological, physiological and genetic investigations blood samples are an indispensable source. However, during breeding season, obtaining blood samples from incubating birds is difficult and time consuming, and trapping in wild populations often restricted in endangered or protected species (KANIA 1992). Even if trapping at the nest-site is feasible, it causes stress that may negatively affect breeding success or even cause nest desertion. It may also alter blood chemistry as levels of plasma corticosterone rise immediately following capture (ROMERO & ROMERO 2002, ROMERO & REED

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2005). Consequently, there is a high interest in minimal or non-invasive techniques to bleed wild birds without catching and handling (BECKER et al. 2006, ARNOLD et al. 2008, BAUCH et al. 2010, BAUCH et al. 2013b).

HELVERSEN & REYER (1984) described a method for obtaining blood from animals using Triatominae bugs, blood-sucking insects belonging to the family Reduviidae which includes *Dipetalogaster maximus* (UHLER, 1894). The efficacy of blood-sucking bugs has since been validated for doubly-labelled water experiments (VOIGT et al. 2003), determination of progesterone, testosterone and hydrocortisone concentrations (VOIGT et al. 2004), serological studies with virus-neutralising antibody titres (VOIGT et al. 2006, VOS et al. 2010), determination of prolactin and corticosterone (ARNOLD et al. 2008, RIECHERT et al. 2012), measurement of a pregnancy hormone in the Iberian Lynx (*Lynx pardinus*) (BRAUN et al. 2009) and recently also for obtaining leucocyte profiles in the animal laboratory on Rabbits (*Oryctolagus cuniculus*) (MARKVARDSEN et al. 2012) and to investigate telomere lengths in avian erythrocytes (BAUCH et al. 2013a).

BECKER et al. (2006) modified this technique for incubating Common Terns (*Sterna hirundo*) by using a blood-sucking bug in a hollow egg. It was also successfully applied to smaller bird species, like Common Swift (*Apus apus*) (BAUCH et al. 2013b). These studies did not find differences in hormone levels obtained via various sampling methods, but the bug-method still needs validation in a field setting (ARNOLD et al. 2008). BECKER et al. (2006) also speculated about a possible effect of the bug's intestinal liquids on the DNA of the focus animal. Overall, the method has the benefit of getting a blood sample without risking haematomas and damage to the blood vessel, which is extremely important in wild animals.

We used the "bug-egg" technique to study a wild urban Eurasian Kestrel population *Falco tinnunculus* in Vienna, Austria (48°12'N, 16°22'E). We tested whether this method is feasible for large-scale extraction of blood samples for (1) individual identification of the breeding bird, (b) microsatellite analysis for paternity tests, and (3) detection of parasites in blood taken from the bug's gut. Kestrels in our study area are non-colonial breeders and their nests are mostly situated in cavities and facades of buildings difficult to access. In that urban setting blood sampling cannot be done within the required three minutes of first disturbance (ROMERO & REED 2005). Hence we also test (4) the use of the blood smears for obtaining leucocyte profiles (Heterophils/Lymphocytes-ratio) as an alternative to the concentration of circulating glucocorticoids as a measure of stress (MÜLLER et al. 2011).

Material and methods

The artificial "bug-egg"

Fieldwork was carried out in 2012. For the construction of artificial Kestrel eggs, we followed the instructions of BECKER et al. (2006). We produced small (35.0 × 29.8 mm) and large eggs (38.5 × 31.0 mm), based on measurements taken in the field in 2010–11 (n = 45), in species-specific colour patterns as evident from eggs in the Bird Collection in the Museum of Natural History in Vienna (Fig. 1). We used epoxy casting resin for the shell and polyurethane foam to make the egg lightest on the side where the bug can pierce the grid. This ensured contact with the incubation patch of the breeding bird also

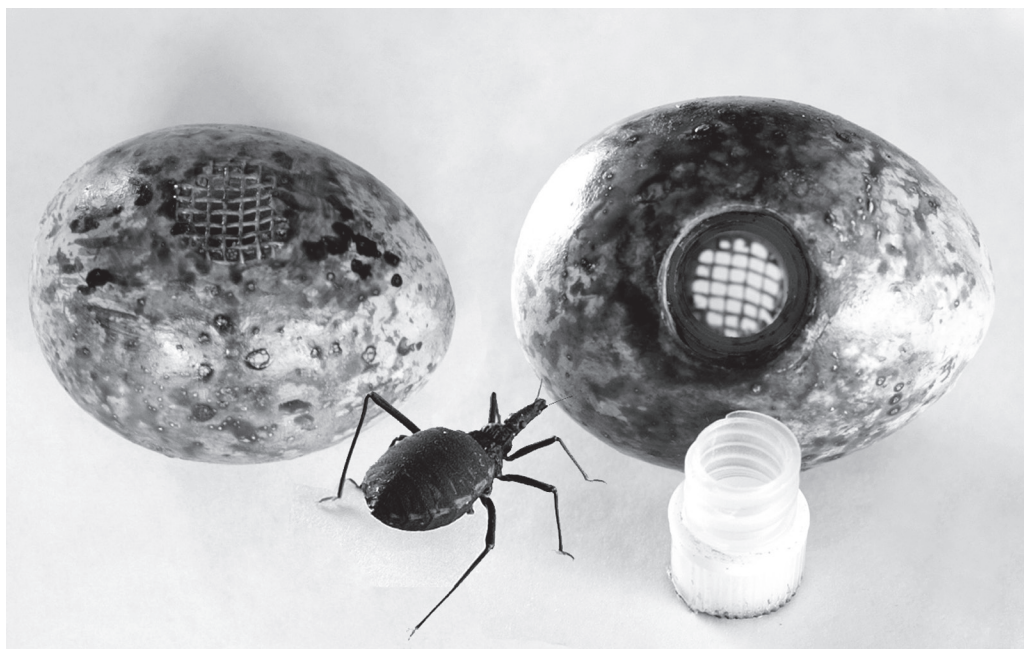


Fig. 1: The artificial egg from top (smaller model, left) and bottom (larger model, right) and fully sucked larval instar L3 of *Dipetalogaster maximus* (photo: G. Witting).

during egg-role behaviour. We wanted to find another solution than additional small holes throughout the shell of the egg (used by ARNOLD et al. 2008 and BAUCH et al. 2013b) to ensure that no sand from the ground of the breeding cavity is blocking the holes and also to increase the stability of the artificial egg.

Since Kestrel nests in the city are hard to reach (mostly via facade and tree climbing) we did not replace the eggs by dummies during the procedure to avoid any damages to the clutch. We just added one artificial egg within the produced clutch, choosing the one closest in size and colour to the existing clutch (Fig. 2) for the same reasons as mentioned before. This was recently also successfully done by BAUCH et al. (2013b) in Swifts.

For the blood-sucking procedure we used starved third larval instars (L3) of *D. maximus* (ordered from AG Zoology/Parasitology, Ruhr-University-Bochum; contact person G.A. SCHAUB). We tested the bug's willingness to sting by presenting a finger at a few centimetres distance. A hungry bug immediately approached with the proboscis erected (see also BECKER et al. 2006). Until application, L3 were kept under laboratory conditions at 27°C and 70% relative humidity. Previous work in Common Terns (BECKER et al. 2006, ARNOLD et al. 2008) showed that a full blood meal could be obtained within 10 min, but the difficult access to Kestrel nests in our study area only allowed a nest check every 3–4 hours. The trial was done at 26 nest-sites between 22 April and 17 June 2012. Bugs were used once.

After collecting the artificial egg, we punctured the bug's abdomen with a needle (Gauge 27, ½ inch) to prepare a blood smear; the remaining sample (100–200 µl) was stored at



Fig. 2: An artificial egg prepared with a blood-sucking bug placed in the middle of a complete Kestrel clutch (6 eggs) in a building cavity in Vienna, Austria (photo: P. Sumasgutner).

-20°C. We also sampled 154 Kestrel chicks by puncturing the brachial vein ("conventional method"). Although the bugs add the protein dipetalogastin as an anticoagulant (LANGE et al. 1999), we stored all samples in EDTA-coated tubes to be able to use the same DNA extraction protocol.

Genetic analysis – sexing and paternity tests

Genetic analysis was conducted at the Laboratory of Molecular Systematics of the Museum of Natural History Vienna. We used the QIAGEN DNeasy Blood & Tissue Kit following standard protocol with Proteinase K to extract DNA. To confirm that we got blood from the incubating female we used the 2718R and 2550F primer set (FRIDOLFSSON & ELLEGREN 1999) on 2% Agarose Gel. For paternity tests we used 14 different microsatellites established for *Falco peregrines* (NESJE et al. 2000) and *Falco naumanni* (PADILLA et al. 2009): NVH fp5, NVH fp79–4, Fnd1.1, Fnd1.2, Fnd1.3, Fnd1.5, Fnd1.6, Fnd1.7, Fnd1.8, Fnd2.1, Fnd2.2, Fnd2.3, Fnd2.4, Fnd2.5. PCR reactions were performed using the QIAGEN Multiplex PCR Kit with 20–60 ng DNA following standard protocol. PCR cycles consisted of an initial activation step at 95°C for 15 min (HotStartTaq DNA Polymerase) and 35 cycles of 94°C for 30 sec, 48°C–57°C annealing temperature for 90 s and 72°C for 90 s, followed by a final extension of 72°C for 20 min. Differences in

final allele sizes and in fluorescent dye labels of primers allowed for pooling multiple loci. The pooled products were then diluted with water 1:20, mixed with HiDiFormamid (Applied Biosystems) and internal size standard LIZ500 and run on an ABI 3130×1 sequencer. All loci were visually identified using the program ABI Peak Scanner 1.0. Final allele sizes were determined using the binning software TANDEM 1.01 (MATSCHEINER & SALZBURGER 2009). CERVUS 3.0 (KALINOWSKI et al. 2007) was used to determine expected (H_E) and observed (H_O) heterozygosities, and the overall probability of identity (PID). MICRO-CHECKER 2.2.3 (VAN OOSTERHOUT et al. 2004) was used to test for the possibility of scoring errors, allelic dropout and null alleles. We included all breeding females and one chick per nest-site (with the purpose to exclude full siblings) in these tests to reduce sampling effects due to relatedness among birds.

Blood-smears – blood-parasites and leucocyte profiles

Immediately after puncturing the bugs' abdomen or the hatchlings' brachial vein a small drop of blood (~10 µl) from the capillary tube was smeared and air-dried on a glass slide directly in the field to prepare a thin blood film. The blood smears were subsequently fixed with absolute methanol and stained with Giemsa's stain (using Hemacolor® Rapid staining of blood smear set). The coloured blood smears were screened by inspecting them under a light microscope at 400× magnification for at least 10 min to see if any blood parasites were visible. Then haematzoa were quantified by counting the number of parasites within 10 000 erythrocytes at 1000× magnification under immersion oil (50–100 fields). The fields were chosen in a line from one end of the slide to the other to compensate for differences in blood thickness across smears. Additionally a complete blood count was done to obtain information about the kinds and numbers of cells in the blood, especially erythrocytes, leucocytes and thrombocytes.

The sampling of nestlings was done at an age of 2–3 weeks. To get relative proportions of each leucocyte type, screening of the blood smear was continued until 100 leucocytes were examined (at 1000× magnification). Within these 100 leucocytes the actual number of heterophils (het), lymphocytes (lymphs), basophils (baso), eosinophiles (eos) and monocytes (mono) were counted. To separate this analysis from the count of haematzoa and the complete blood count we use the term leucocyte profile.

Results and discussion

Blood samples via blood-sucking bugs

Twenty-six nests were tested with bugs of which starvation time before the trial varied between 2–8 weeks, resulting in 21 samples from breeding females. For bugs with a starvation time of 2–4 weeks, success rate of blood-sucking in eight nests was 1 out of 8 after 3–4 h, with another three after 6–8 h and three more after 10–12 h (replacing the bug after each nest check). After 6–8 weeks of bug starvation, success rate was markedly higher with 14 out of 18 having sucked blood within 3–4 h of exposure (summary on success rate in Table 1). STADLER et al. (2011) provided a detailed description how to raise and keep blood-sucking bugs, including the instruction that L3 can be used from 3–6 weeks after hatching onwards. In our trial we needed to extend that starvation time up to 6–8 weeks to successfully collect blood samples.

We found no visible response of the bird to the bug bite, but only two nest-sites could be directly observed during the whole trial period. In one case (3.4%) out of 26 trials the incubating bird disposed the artificial egg by removing it from the nest cup and destroying it. In general animals exposed to *D. maximus* do not seem to react to the bite, probably due to the small diameter of the proboscis (20 µm, smaller than a 26 Gauge needle) or to anaesthetic saliva being injected into the wound (MARKVARSEN et al. 2012). The use of this method had no negative effect on breeding success, as all chicks hatched successfully.

Sexing and paternity tests

In Eurasian Kestrels the sequence on the Z chromosome measures 484 base pairs (bp) and on the W chromosome 295 bp (NITTINGER 2004). The difference of 189 bp was sufficiently long to detect both fragments on a 2% Agarose gel, without any visible relicts of DNA of *D. maximus*. Since the female is the heterogametic sex in birds, results show two bands for female blood, one band for male blood, but also two bands for a mixture of both. In kestrels risk of such a contamination remains low, since it is mostly the female incubating (VILLAGE 1990). A contamination would anyhow become visible on peak scan in our further analyses, which was apparently the case in 3 out of 21 samples we consequently excluded.

Four loci displayed significant deviations from Hardy–Weinberg equilibrium (P_{HWE}) or significant probability of null alleles (P_{null}): NVH fp79-4 ($P_{HWE} = 0.0311$, $P_{null} = 0.1435$), Fnd1.2 ($P_{HWE} < 0.0001$, $P_{null} = 0.0999$), Fnd1.6 ($P_{HWE} < 0.0001$, $P_{null} = 0.0505$) and Fnd1.8 ($P_{HWE} = 0.0011$, $P_{null} = 0.1902$). These loci were not used in further analysis. Our Kestrels

Table 1: Success rate of the blood-sucking bug *Dipetalogaster maximus* in collecting blood samples in Eurasian Kestrels (*Falco tinnunculus*) in Vienna, Austria in 2012, dependent of starvation and exposure time of the bug compared to cited bird studies using the bug-method: (+) successful, (-) not successful.

Species		Success rate dependent on starvation and exposure time			
<i>Falco tinnunculus</i>	Exposure time:	3–4 h	6–8 h	10–12 h	
	Success rate:	+ / -	+ / -	+ / -	
	2–4 weeks starvation	n = 1 / 7	n = 3 / 4	n = 3 / 1	
	(n = 8 nests)	12.5%	42.9%	75%	
	6–8 weeks starvation	n = 14 / 4	- / -	- / -	
	(n = 18 nests)	77.8%			
Species	Exposure time	Success rate	Starvation	Study	
<i>Sterna hirundo</i>	60 min	34% (n = 163)	no details	BECKER et al. 2006	
<i>Sterna hirundo</i>	30 min	89.5% (n = 14)	no details	C. BAUCH unpubl. (in ARNOLD et al. 2008)	
<i>Sterna hirundo</i>	30 min	86.1 (n = 34) 82.2% (n = 44)	no details	BAUCH et al. 2010	
<i>Apus apus</i>	60 min	40% (n = 27)	no details	BAUCH et al. 2013b	

showed polymorphism at all 10 tested loci, with the number of alleles per locus ranging from 8 to 16 and observed heterozygosities ranging from 0.570 to 0.882. With the remaining 10 microsatellites the females proved to be the genetic mother in all sampled nests, as also determined with the excluded loci Fnd1.2, Fnd1.6 and Fnd1.8, but not with locus NVH fp79–4. The "bug-method" can be used for the purpose of paternity tests, since we found no sign of the bug's DNA influencing the results.

Blood-parasites

We prepared 21 blood smears with the bug-method from breeding females and 154 with the conventional method from chicks. The screening of the blood-smears showed different qualities depending on the duration the bug-egg was left inside the nest: blood smears prepared after 3–4 h bug-egg's exposure in the nest were high in quality for blood-parasite counts. We only included these 15 samples in further analysis, since samples prepared after more than 6 hours contained a high quantity of lysed blood cells making it impossible to count infected red blood cells and to differentiate between different kinds of white blood cells to prepare a viable leucocyte profile (Table 2). VOIGT et al. (2004) experimented on digestion by bugs, showing an increased variation after 4 h of the blood meal. Even though the authors recommended using the sampled blood before 8 h after sampling for analysis, we needed to shorten that time in our study.

We detected *Haemoproteus* sp. in 46.7% of adult breeding females (range of infected red blood cells within 10 000 erythrocytes: 13.7–34.1, median 21.0). For two *Haemoproteus* positive females we had samples collected via the bug method and the conventional method, revealing the same results: 16.0 vs. 20.7 parasites found in 10 000 erythrocytes on the smear and 34.0 vs. 34.1. Unfortunately, parasite prevalence in blood slides of

Table 2: Mean values (\pm SD) for complete blood counts within 10 000 erythrocytes and leucocyte profiles (Heterophils/Lymphocytes-ratio) within 100 leucocytes for breeding female Kestrels (*Falco tinnunculus*) in Vienna, Austria in 2012.

	Blood samples obtained via the bug-method		t-value	P-value	Significance
	Females (n = 8)	Females (n = 7)			
	<i>Haemoproteus</i> (-)	<i>Haemoproteus</i> (+)			
within 10 000 erythrocytes					
Leucocytes	65.3 (\pm 31.8)	119.7 (\pm 103.4)	-4.48	0.0005	***
Thromocytes	2.6 (\pm 4.8)	15.1 (\pm 10.1)	-3.52	0.0034	**
within 100 leucocytes					
het	20.7 (\pm 12.8)	8.7 (\pm 8.3)	-4.57	0.0004	***
lymphs	73.3 (\pm 18.2)	86.6 (\pm 11.7)	-16.24	<0.0001	***
baso	0.6 (\pm 0.8)	2.2 (\pm 4.4)	-1.56	0.142	NS
eos	4.8 (\pm 4.9)	1.8 (\pm 3.0)	2.67	0.0182	*
mono	0.6 (\pm 1.1)	0.7 (\pm 1.3)	-0.49	0.6325	NS
H/L ratio	0.3	0.1	1.05	0.3103	NS

Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, 'NS' not significant.

nestlings was nil, as we expected, because it takes at least 1–2 weeks for the parasites to be visible in the blood stream after infection of the nestling (KORPIMÄKI et al. 1995). We presume that chicks older than two weeks might be infected with blood parasites but at very low prevalence. Parasites may not yet be fully developed in the blood cells, but their DNA might be detectable using PCR based methods instead of smears (TOMÉ et al. 2005, DELGADO-V & FRENCH 2012).

Leucocyte profiles

To our knowledge there is only one study on haematology in blood sampled either via blood-sucking bugs or the conventional method done in laboratory with Rabbits (MARKVARDSEN et al. 2012) and none in wild animals where the exposure time is harder to be standardised. Results therein have shown significantly higher levels of neutrophils, lymphocytes, basophils and monocytes in blood samples collected by the conventional method, concluding that a mixture of both methods is not accurate for H/L ratios. This difference might relate to (1) the metabolism of the bug, and/or (2) the bug blood samples originating from either a vein or an artery (see also LUE et al. 2007; conventional blood samples are collected from the veins). The study further concluded the exposure of the animal to bug antigens as unlikely to induce an immune response, since measured levels in leucocyte profiles should then have been higher in bug blood samples rather than the other way around. Since we only have both sampling methods for two individuals (results showed the exactly same H/L ratio for bug- and conventional-samples with a ratio of 0.02 for one and of 0.05 for the other female) we present results revealed via the bug method in incubating females. The H/L-ratio between infected (+) and *Haemoproteus* free (-) blood was not significantly different, but a logistic regression with the actual number of parasites in 10 000 erythrocytes and the H/L ratio showed a significant correlation: $R^2 = 0.29$, $F(1,13) = 5.28$, $P = 0.039$ of a lower H/L ratio in higher infected females. We further received significant values for less heterophils and eosinophils and more lymphocytes in *Haemoproteus* (+) individuals (Table 2) which are the basic measures resulting in the H/L ratio.

Conclusion

Our experiences have shown that the adaptations for the artificial eggs had clearly positive effects for the kestrel project. Using two materials with different density insured that the artificial eggs had a defined centre of mass and the opening with the L3 was always facing upwards, even during egg-roll behaviour. This method proved to be superior to fixing the artificial egg on the nest ground because it did not hinder the egg-roll behaviour of the female Kestrel and provides an alternative to holes all around the egg shell which might be problematic in a sandy breeding niche or when a higher stability is required. We can conclude that the stinging success of the L3s after 6–8 weeks of starvation was very high with 77.8%. A shorter starvation time failed in our trial, which was previously only mentioned by MARKVARDSEN et al. (2012) who used bugs fasted for 5 weeks prior to the study and failing to sting in their experiment. Further, the method is very useful for the purposes of microsatellite analyses and blood parasite counts, as long as the artificial bug-egg is retrieved not later than 4 h from the Kestrel clutch. For H/L ratios we clearly need further evaluations for differences in results obtained via the bug-method and the conventional method. In respect to applications necessary for field work,

our modifications proved unnecessary to replace all eggs with dummy eggs during the experiment making the procedure reasonably time-saving and safer in terms of preventing Kestrel eggs to be damaged or cooling during facade and tree climbing.

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Part 2

Chapter V - preliminary results: Genetic variability in Eurasian kestrels (*Falco tinnunculus*) in Vienna, Austria.



Photo: Norbert Jalitsch

Genetic variability in Eurasian kestrels (*Falco tinnunculus*) in Vienna, Austria

Brief introduction

Genetic analyses are necessary to investigate whether urban kestrel population experienced a 'bottleneck' when it was founded and whether the urban population is genetically isolated and the expansion process driven entirely by urban-fledged individuals. For that purpose I compared kestrels breeding in the west of Vienna and individuals from the east with each other. The western individuals are using the historical building structure in the centre for nesting, while the eastern individuals are using a heterogeneous habitat of new buildings and family homes, forest patches and fields for nesting and as hunting area. So far I do not know if gene flow between the city (west) and adjacent periphery (east) exist. Further I have material available at the Natural History Museum Vienna from kestrels found in the surrounding rural areas of Austria. I restricted the tissue samples on individuals found during breeding season and will use the data as an out-group in the study to identify directions of gene-flow.

Although the female highly relies on a strong pair-bond for successful breeding, due to the higher territory density, extra-pair copulation may be more frequent in urban environments. In a running project I focus on kinship in urban Kestrels, especially (a) the number of paternities in one brood to investigate (b) the effect of extra-pair copulation and (c) parental investment along the urban gradient. The degree of relatedness may correlate with some ecological traits, such as a higher re-occupation rate or high site fidelity (Riegert et al. 2010). I expect individuals breeding near the city centre to be more related to each other than individuals from the periphery (in the east).

Material and methods

In the genetic analysis I used the QIAGEN DNeasy Blood & Tissue Kit following the standard protocol with Proteinase K to extract DNA. Sex identification was done using the *2718R* and *2550F* primer set (Fridolfsson and Ellegren 1999) and confirmed with the *Falco* specific *fp102* and *fp49* primers (Nesje and Røed 2000). For paternity tests and individual heterozygosity I used 14 different microsatellites established for *F. Peregrines* (Nesje et al. 2000) and *F. naumanni* (Padilla et al. 2009): *NVH fp5*, *NVH fp79-4*, *Fnd1.1*, *Fnd1.2*, *Fnd1.3*, *Fnd1.5*, *Fnd1.6*, *Fnd1.7*, *Fnd1.8*, *Fnd2.1*, *Fnd2.2*, *Fnd2.3*, *Fnd2.4*, *Fnd2.5*. PCR reactions were performed using the QIAGEN Multiplex PCR Kit with 20-60 ng DNA following the standard protocol. PCR cycles consisted of an initial activation step at 95°C for 15 min (HotStartTaq DNA Polymerase) and 35 cycles of 94°C for 30 sec, 48°C-57°C (48°C for *Fnd1.7*, 50°C for *NVH fp79-4*, *Fnd1.1*, *Fnd1.2*, *Fnd1.5*, *Fnd1.6*

and *Fnd2.1*, 53°C for *Fnd1.8*, *Fnd2.3* and *Fnd2.4*, and 57°C for *NVH fp5*, *Fnd1.3*, *Fnd2.2* and *Fnd2.5*) annealing temperature for 90 s and 72°C for 90 s, followed by a final extension of 72°C for 20 min. Differences in final allele sizes and in fluorescent dye labels of primers allowed for pooling multiple loci. The pooled products were then diluted with water 1:20, mixed with HiDi-Formamid (Applied Biosystems) and internal size standard LIZ500 and run on an ABI 3130x1 sequencer. All loci were visually identified using the program ABI PeakScanner 1.0. Final allele sizes were determined using the binning software Tandem 1.01 (Matschiner and Salzburger 2009). Ambiguous samples were re-genotyped up to three times. CERVUS 3.0 (Kalinowski et al. 2007) was used to determine expected (H_E) and observed (H_O) heterozygosities and the overall probability of identity (P_{ID} , results not shown). GENEPOP 4.2 (Raymond and Rousset 1995; Rousset 2008) was used to determine departures from Hardy-Weinberg equilibrium at each locus, to test for null alleles, to calculate probability tests for genotypic linkage disequilibrium between loci and to determine the inbreeding coefficient F_{IS} . MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004) was used to test for the possibility of scoring errors, allelic dropout and null alleles. I used the R package ‘PopGenReport’ to visualize the population genetic data (Adamack and Gruber 2014).

For further sibship analysis I will use software COLONY 2 (Wang and Santure 2009), a likelihood-based method implementing a group-wise approach for sibship reconstruction. For these sibship inferences the full likelihood model will be used.

Preliminary results and discussion

I analysed 150 individuals (one chick per nest per year, full siblings are also among years excluded from the study). The mean number of alleles per locus (across all locations) was 12.4; the percentage of missing data was 3.7% (summary data in Table 1). I compared individuals from the west ($n = 107$) and east ($n = 43$) of Vienna with each other, using the river Danube as a potential barrier due to different building and habitat structure in the west and the east of the city. In the allelic richness summary statistics I found mean allelic richness in the western individuals of 9.55 and in the eastern individuals of 9.78 (no significant difference).

Tab. 1: Summary data of 14 microsatellites developed from *F. peregrinus* (*NVH fp*, Nesje et al. 2000) und *F. naumanni* (*Fnd*, Padilla et al. 2009). Size range (base pairs bp), N_A = number of alleles, H_O = observed heterozygosity, H_E = expected heterozygosity and P_{IC} = mean polymorphic information content shown from cross amplification in *F. tinnunculus* in this study. Results were generated in CERVUS.

Locus	Primer sequences (5'–3')	Size range (bp)	N_A	H_O	H_E	P_{IC}	GenBank no.
<i>NVH fp5</i>	F:CCGTTCTGGAGTCAAAAC R:CATGCAGCACTTTATTCAG	102-118	9	0.85	0.827	0.801	AF118420
<i>NVH fp79-4</i>	F:TGGCTTCTCTATCAGTAAC R:GGCTGGGTGGAATTAAAG	126-156	15	0.631	0.851	0.831	AF118427

Locus	Primer sequences (5'–3')	Size range (bp)	N_A	H_O	H_E	P_{IC}	GenBank no.
<i>Fnd1.1</i>	F: TCACCTGCTTCTTGCTTCT R: CCAAACCTCTCTTTCCAGA	244-264	6	0.357	0.357	0.322	FM180205
<i>Fnd1.2</i>	F: GCAGTCTTGACAGATGGCTTT R: TGAAGTGTGACTCCGCTATGA	150-182	16	0.727	0.858	0.839	FM180206
<i>Fnd1.3</i>	F: GCCTAAGGTTTCCCTCAGCTA R: TCATCAGACTGCAAACTGGA	198-232	15	0.875	0.852	0.833	FM180207
<i>Fnd1.5</i>	F: CCATTGATTTTCATCAACTACA R: CCTGTTGAGAATGCGTGAAA	219-243	12	0.759	0.805	0.783	FM180210
<i>Fnd1.6</i>	F: ATTTGTGGCAAACAGAGGA R: CCCACATTTTCCAAACAAGG	302-356	25	0.847	0.928	0.919	FM180211
<i>Fnd1.7</i>	F: TACCGTCTTGTTGGAAGT R: CTACAGTCTGCCCCAAGAA	229-245	7	0.661	0.647	0.585	FM180212
<i>Fnd1.8</i>	F: CAGTGACGCTGAAAGATGA R: GCTTGGAAGTCCTCTGCTG	179-207	8	0.414	0.672	0.633	FM180213
<i>Fnd2.1</i>	F: AGTCATGGCTTCCGATCAAG R: TCAGGCAGCCTATTTTTGG	185-207	12	0.848	0.861	0.841	FM180214
<i>Fnd2.2</i>	F: AACTTTGCCCCAGATCACAC R: GCACAGAGACCCCGTTACAT	182-298	8	0.566	0.601	0.548	FM180215
<i>Fnd2.3</i>	F: CAAGCAGGGTGAAAATCCAT R: GTTTTCCCTCATTGCCTGAA	219-249	9	0.6	0.605	0.564	FM180216
<i>Fnd2.4</i>	F: ACCACAGGTGCTTTTTCACA R: AAAAGAAATGGTGGCAGGTG	165-179	7	0.664	0.698	0.665	FM180217
<i>Fnd2.5</i>	F: CACTACCAGCCCTGAACCAT R: CTTCTTGACAGGGGTGTGGT	207-239	14	0.814	0.801	0.772	FM180218

Four loci displayed significant deviations from Hardy–Weinberg equilibrium (P_{HWE}) or significant probability of null alleles (P_{null}): *NVH fp79-4* ($P_{HWE} = 0.0311$, $P_{null} = 0.1435$), *Fnd1.2* ($P_{HWE} < 0.0001$, $P_{null} = 0.0999$), *Fnd1.6* ($P_{HWE} < 0.0001$, $P_{null} = 0.0505$) and *Fnd1.8* ($P_{HWE} = 0.0011$, $P_{null} = 0.1902$). These loci will not be used in further analysis.

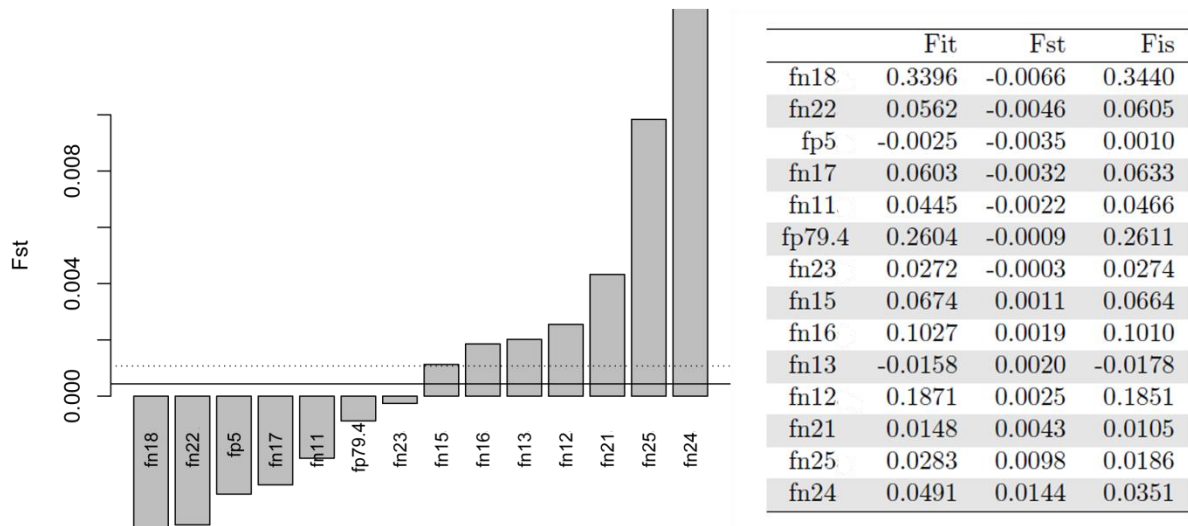


Fig. 1, Table 2: Fst across entire population at each locus; and population wide Fit, Fst, and Fis values for each locus. The table is sorted in ascending order based on Fst. Solid line shows median Fst, dotted line shows mean Fst, dashed lines indicate 2.5th and 97.5th percentiles of Fst.

So far I have not found any differences between the western city kestrels and the eastern individuals breeding in the periphery of Vienna (Fig. 2).

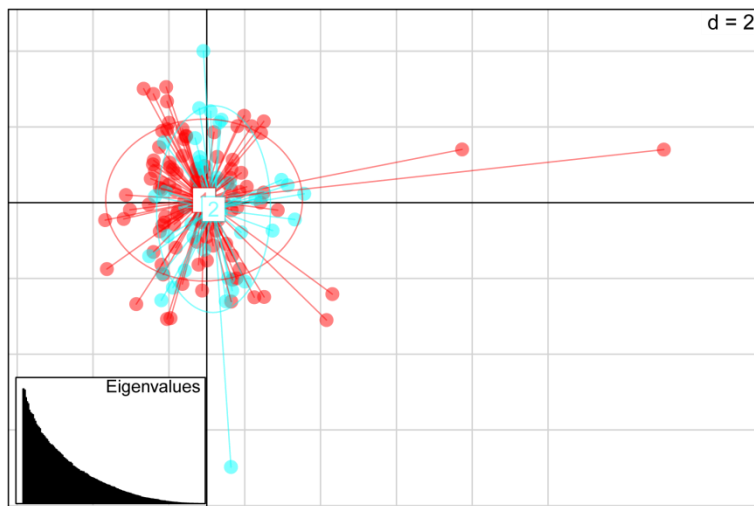


Fig. 2: Principal coordinate analysis, using the first two axes, visualising genetic diversity among sampled individuals. Missing data are replaced by the mean of the allele frequencies. Colours indicate ‘subpopulation’: 1 – red, city in the west; 2 – cyan, periphery in the east.

Populations separated by different life styles or geography may lead to genetic differentiation. The urban population of Viennese kestrels ecologically differs in many ways from their suburban counterparts. They occupy nesting sites on building cavities, have lower reproductive output (Sumasgutner et al. *accepted*; Sumasgutner et al. 2014) and show different foraging behaviour (Sumasgutner et al. 2013). However, I did not yet find any marked genetic differences between the studied ‘subpopulations’. Kestrels in the city and the periphery showed similar degree of genetic polymorphism (details not shown), which is in line with studies in Warsaw and a small city in Southern Bohemia (Riegert et al. 2010; Rutkowski et al. 2006). Rutkowski also reported higher genetic variability for rural populations and supposed that gene flow from the rural kestrel population to the city might be stronger than vice versa. My preliminary results do not agree with these findings. The allelic richness of the kestrel populations studied in Vienna was similar and the F_{st} values (Table 2) were very low.

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Part 3

Chapter VI: Sumasgutner P, Vasko V, Varjonen R, Korpimäki E (*submitted*) Public information revealed by prey remains in nest-sites is more important than ectoparasite avoidance in the settlement decisions of Eurasian kestrels (*Falco tinnunculus*). — Behavioral Ecology and Sociobiology.



Photo: Petra Sumasgutner

Public information revealed by prey remains in nest-sites is more important than ecto-parasite avoidance in the settlement decisions of Eurasian kestrels

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Abstract

Animals constantly need to acquire information about the environment for settlement decisions, either by using a trial-and-error strategy or by using public information by monitoring conspecifics. We studied a nest-box population of Eurasian kestrels *Falco tinnunculus* in western Finland to test if pellets and other prey remains accumulated on the bottom of nest-boxes are used as public information during settlement. During 2002-2013 nest-boxes were randomly cleaned (treatment) or left un-cleaned (control) in each season. It is possible that kestrels reuse nest-boxes which include information of successful nesting (i.e. have not been cleaned) because they indicate previous breeding attempt at the site. At the same time this decision may entail costs because of blood-sucking ecto-parasites like *Carnus hemapterus* overwintering in the layer of prey remains. First, we found that egg-laying date was significantly earlier in un-cleaned control boxes than in cleaned treatment boxes, indicating the use of public information revealed by prey remains in the settlement decision. Second, the ecto-parasite burden of young nestlings (age 6-15 days) was significantly higher in un-cleaned control nest-boxes, without however having any obvious influence on breeding success. In conclusion, the use of prey remains revealing successful breeding attempt of the previous year as public information appeared to be important in the settlement decision of kestrels. Our study thus supports the public information hypothesis, but not the ecto-parasite avoidance hypothesis, because control nest-boxes with higher ecto-parasite burden were occupied earlier in the season than cleaned nest-boxes with lower ecto-parasite burden.

Keywords: raptor, social information, indirect cue, previous breeding attempt, nest-site selection, *Carnus hemapterus*

1. Introduction

To understand breeding habitat selection, it is necessary to examine how individual animals assess the environmental quality and the suitability of a future breeding site. Animals constantly need to acquire information about the environment for settlement decisions, either by using direct cues, like food or nest-site availability (the ‘direct assessment hypothesis’), or indirect cues, such as the presence of conspecifics (the ‘conspecific attraction hypothesis’, Stamps 1994) and their productivity in the previous year (the ‘public information hypothesis’, Danchin et al. 1998, Doligez et al. 2003). Using personal information in a trial-and-error strategy may be more costly in terms of time and energy (Kendal et al. 2005) compared to social information by monitoring others (Dall et al. 2005; Valone and Templeton 2002). In fact, copying decisions of other individuals seems to be a common strategy in birds used in various circumstances, including foraging, in which context the public information hypothesis was originally developed (Valone 1989), habitat selection (Doligez et al. 2002) and nest-site selection (Kokko et al. 2004).

In avian research, one way of investigating the mechanisms involved in nest-site selection is to examine breeding success and habitat characteristics in terms of animals returning to a location where they have already reproduced. This has been analysed in colony breeders (Aparicio et al. 2007) and also in solitary breeders with a high nest-site tradition (Hoi et al. 2012). Another way is to investigate factors promoting nest-site establishment and abandonment as it has been studied in nest-building raptor species (the Black kite *Milvus migrans*) (Sergio and Penteriani 2005). Indirect information on habitat quality is especially important when individuals cannot evaluate previous breeding success by direct observation on the nesting attempt, which might be due to large home range sizes, non-overlapping territories or to a high turn-over rate in the breeding area (Kokko and Sutherland 2001). In this case, nest material, faeces, pellets and other prey remains might act as visible cues for raptors indirectly indicating a previous breeding attempt. Hence, it is possible that raptors reuse nests of conspecifics using those pellets and prey remains and not the actual productivity of conspecifics in the previous year as public information. At the same time this decision may entail costs due to ecto-parasites overwintering in the nest material, increasing the risk of ecto-parasite infestation and nestling mortality (Wimberger 1984). Parasite infestation may further delay clutch initiation and induce smaller brood sizes at hatching, higher nest desertion (Oppliger et al. 1994) or reduce parental investment (Christe et al. 1996; Fitze et al. 2004; Tripet and Richner 1997). The so-called ‘ecto-parasite-avoidance hypothesis’ is one of the hypotheses to explain the alternative nest-using behaviour of raptors (see Ontiveros et al. 2008) and act therefore as an alternative to the public information hypothesis.

We conducted a field experiment in solitary breeding Eurasian kestrels (*Falco tinnunculus*, hereafter kestrel) on the use of pellets and prey remains as public information in settlement

decisions. The kestrel is a good candidate for testing this hypothesis because (1) of its inability to build a nest (Village 1990); kestrels reuse suitable nest-sites making it possible to manipulate indirect cues for previous breeding success on the sites offered. (2) In North Europe, kestrels are long-distance migrants and have therefore a short time-window for settlement decisions. In most bird species breeding in temperate ecosystems productivity of eggs and fledglings decline with laying date, which has also been shown for kestrels (Korpimäki and Wiehn 1998). Hence, time for direct habitat assessment is limited, favouring the utilisation of indirect cues for settlement decisions (Sergio and Penteriani 2005). (3) In our study population in Finland, breeding parent kestrels have a high turn-over rate and therefore low nest-site tradition (Vasko et al. 2011) making direct observation of previous breeding success on the site very unlikely (the 'traditional' definition of public information).

In this study, we aim to determine whether the use of public information (hypothesis 1) or ecto-parasite avoidance (hypothesis 2) is important in the nest-site selection of kestrels. First, we examined the basic assumptions that previous breeding success at a nest-site is used as public information in the following year, to settle in a nest-box. For this purpose we carried out an experiment over an 11-year period (autumn 2002 to summer 2013) with randomly cleaned treatment and un-cleaned control nest-boxes to manipulate indirect cues that kestrels could use for determining previous breeding success at a nest-site, namely the presence or absence of pellets and other prey remains in the nest-box. In case of hypothesis 1 we predict higher occupation rates and/or earlier egg-laying dates and larger fledged brood sizes in un-cleaned than in cleaned boxes. Secondly we tested the influence of ecto-parasites on breeding success. Cleaned treatment nest-boxes should be less infested by ecto-parasites than un-cleaned control nest-boxes. In case of hypothesis 2 we predict higher occupation rates and/or earlier egg-laying dates in cleaned than in un-cleaned boxes. If nest-site selection mechanisms have evolved to inhibit ecto-parasite infestations, pairs that use un-cleaned control nest-boxes should have further decreased breeding success compared to pairs that settle in cleaned nest-boxes. Hence, we test the public information hypothesis and the ecto-parasite avoidance hypothesis against each other.

2. Material and Methods

2.1. Study area and experimental design

The study area is situated in the Kauhava and Lapua region, western Finland (62°59'-63°10'N, 22°50'- 23°20'E). Within the study area, from autumn 2002 to the breeding season 2013, 35 to 119 kestrel nest-boxes were included each year in an experimental setup (mean = 78.6, *SD* = 31.4). We randomly assigned each nest-box to one of two following groups: treatment (pellets and prey remains were removed and hay and straw as nest material were renewed, hereafter

clean nest-box; $n = 366$) or control (pellets, prey remains and old nest material were left inside, hereafter un-cleaned nest-box; $n = 498$). The manipulation was done in late September after the breeding season. The randomisation was given by flipping a coin each morning at the first box of the inspection round. Thereafter, every other nest-box was cleaned or left un-cleaned accordingly as the inspection of the boxes preceded, thus also resulting in an even spatial distribution of cleaned vs. un-cleaned boxes.

In all analyses we solely included nest-boxes which fledged at least one young the year before to ensure that prey remains inside the box were from the previous breeding season, reducing the sample size to 363 cleaned and 417 un-cleaned nest-boxes (a total of 780 boxes). In some cases, the old nest-box had to be replaced by a new clean one because of its bad condition. We excluded these nest-boxes from our study, because new boxes may include, for example, less ectoparasites overwintering than old ones, and the coloration of the new box is usually brighter. The nest-boxes slightly varied in size (between 25-30 x 25-30 cm base, 25-30 cm height), mounted 5 to 6 m above ground on the gables of barns, and sometimes on telephone posts or solitary trees when no barns were available. In our study area, clutch size of kestrels is not related to the orientation and to the bottom area of the nest-box (Valkama and Korpimäki 1999). Additionally, a high annual turn-over rate is known for kestrel parents breeding in our study site (on average 90% of female parents and 68% of male parents are new every year), together with a high divorce rate, with 82% of those female parents that returned to breed in the study area mating with a different male the next year (pooled data from 1985 to 2010 for females whose previous partner was documented to be still alive, see Vasko et al. 2011 for details). Further, the percentage of young breeders (breeding in their 2nd calendar year) is very low (Laaksonen et al. 2004). Inter-sexual 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.

2.2. Kestrels under fluctuating food conditions

The main prey items of kestrels in our study site are voles of the genera *Microtus* (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*) and *Myodes* (the bank vole *M. glareolus*, Korpimäki 1985). Because the abundance of main prey of kestrels is expected to be highly determined by the phase of the three-year vole cycle (Hansson and Henttonen 1985), vole abundance indices were estimated by bi-annual trapping from autumn 2002 until spring 2013. Snaptraps were laid out in mid-September (autumn) and in early May (spring) in four sample plots in the study area, located in four main habitat types: cultivated field, abandoned field, spruce forest and pine forest (Korpimäki et al. 2005). Between 50 and 100 Finnish metal mouse snaptraps were set at 10 m intervals in vole runways on each plot. They were baited with mixed-grain bread and were checked once a day for 4 days. Thus, the area of a sample plot ranged from

0.5 to 1.0 ha. We pooled the results from 4 night trapping periods and standardised them to the number of animals caught per 100 trap nights (Korpimäki and Wiehn 1998) in each habitat type. These data are thereafter mentioned as vole index in spring and vole index in autumn.

2.3. Kestrels and their ecto-parasites

The most significant arthropod ecto-parasites present in bird nests are mites and ticks (Acarina), and insects like bugs (Hemiptera), fleas (Siphonoptera) and flies (Diptera) (Hansell (2000). In kestrels, the most abundant ecto-parasite is the blood-sucking fly *Carnus haemapterus* (Piechocki 1982). Adult individuals are hematophagous parasites and can mostly be found on bald areas of skin, usually under the wings while larvae are saprotrophic and thought to live in the nesting material until they pupate and move onto a host afterwards (Grimaldi 1997).

The level of infestation increases from birth to 13 days of age (mean 10.8 ecto-parasites/nestling, max. 55, $n = 73$ chicks), then declines and, at fledging, nestlings are virtually free of parasites (> 23 days old, $n = 23$ chicks, pooled data for ecto-parasite screening in 2011 and 2012, P. Sumasgutner and E. Korpimäki unpublished data). This can be linked to the development of the plumage of chicks (Kaľavský and Pospíšilová 2010). When ecto-parasites are still rare in the first days after hatching, *C. haemapterus* are mainly located on the first-hatched nestlings as known from barn owls (*Tyto alba*), but, as nestlings grow up, parasite intensity increases and the last-hatched nestlings become the most infested ones (Roulin et al. 2003). Kestrels living in nest-boxes are more likely to be infested by ecto-parasites than conspecific pairs living in other types of nests (Fargallo et al. 2001). We examined exclusively kestrels breeding in nest-boxes.

2.4. Morphometric measurement and ecto-parasite screening

From the beginning of the breeding season (from late April on) nest-boxes were monitored to record the occupancy of nest-boxes, egg-laying date, clutch size, number of hatched offspring and number of fledged young of all active nests. Breeding success was defined as the number of fledglings raised per nest per year, and hereafter named as fledged brood size. If possible, parents were ringed and aged as yearlings (2nd calendar year) or adults (3rd calendar year and more) according to Village et al. (1980) and Forsman (1984). We used the residuals of egg-laying date (residuals from lay date by year regression) to compare differences in the laying date among treatment and control nest-boxes. To analyse the fledging rate we used the proportion of fledged young (relative to the number of eggs), to ensure that results are not biased by carry over effects of the clutch size.

During every visit at the nest-box, the chicks were systematically screened for ecto-parasites in 2012. The last screening was done before the chicks were ringed (max. age 25 days). During examination, we did not remove the ecto-parasites, to avoid any manipulation of breeding suc-

cess. We measured wing length of nestlings for age determination if the exact age (in days) was not known from direct observations at hatching.

To calculate the ecto-parasite burden for statistical analysis we ranked the chicks within the brood in 1-senior (first-hatched) sibling, 3-junior (last-hatched) sibling and 2-all the other chicks in between. This ranking allowed using all information collected from one nest-box, but ensured that every chick is just appearing once in the analysis to avoid any pseudo-replication. The ecto-parasite burden per nest-box was defined as the mean value of ecto-parasites per chick within a brood for two consecutive visits (age range of chicks 1-15 days). This was the most standardised method feasible during field work to get a value for the ecto-parasite burden without manipulating the nest-box. An actual count of ecto-parasites per nest-box would require a complete removal of the nesting material during breeding season and therefore a high disturbance and increased probability of nest desertion. A count close to the fledging phase seemed also not reasonable since ecto-parasite infestation of chicks decreases after 15 days.

2.5. Statistical analysis

2.5.1. Public information

We performed generalized linear mixed models (GLMM) on occupancy and breeding parameters, where treatment (cleaned vs. un-cleaned nest-boxes) was included as the explanatory variable. We used the R packages 'lme4' (Bates and Maechler 2009) and 'lmerTest' (Kuznetsova et al. 2013) for the mixed model design. We included the nest-box ID and the study year as random factors to avoid pseudoreplication (Hurlbert 1984). Nest-box ID was used due to repeated sampling of some nest-boxes over years. Study year as random factor allowed us taking temporal variations (e.g. weather conditions) into account, which were not included as explanatory variables in the models. Error family was chosen according to the type of response variable: gaussian family and identity link function for egg-laying date, poisson error family and log link function for clutch size and fledged brood size, and binomial error family and logit link function for occupation and the ratio of successfully fledged per egg laid. We did not include a random factor for individual identity of breeding adults because the annual turnover rate of parents is very high in this northern population (90.4% of females and 74.8% of males are first-time breeders in the study area (Vasko et al. 2011)). However, we cannot ignore the slight possibility that kestrels observed their conspecifics during the previous breeding season and knew which neighbouring nest-site had been successful before. Therefore we solely used nest-boxes which have previously been successful and included the number of fledged young (fledged $t-1$) as covariate. We preferred the actual number of fledged young over a factor variable successful/not successful because more pellets and prey remains could also be a cue for higher breeding success. Pellets and other prey remains accumulate in the last two weeks of the nestling-period, and more nestlings obviously produce more pellets. Alternatively to the variable fledged $t-1$, we included

the laying date of the previous year (laying date $t-1$) relative to the population mean of each year to take possible individual differences of the nest-site into account (early/late boxes could always be early/late because of some microhabitat differences in the surroundings not obvious for us).

A significant influence of the age of the breeding adults on egg-laying date and clutch size is known from our study population of kestrels (Korpimäki and Wiehn 1998). From 353 occupied nest-boxes we could trap, ring and age 295 females and 244 males, among which 18.9% and 4.1% respectively were yearlings (i.e. in their 2nd calendar year). In total we knew parental ages of both sexes for 194 nest-boxes included in our results.

We evaluated models that included the following covariates: treatment, vole index in spring t , vole index previous autumn $t-1$, number of fledged $t-t$ or laying date $t-1$, parental age, interaction treatment x vole index and treatment x parental age. All covariates were tested for correlation of fixed effects and a resulting set of uncorrelated explanatory variables were fitted to a maximal model, extracted one by one, and associated changes in the model deviance assessed by a likelihood ratio test (Zuur et al. 2009). At each step, we calculated the AIC (Akaike Information Criterion) and considered as final model the one with the lowest value (Burnham et al. 2011).

2.5.2. Ecto-parasite avoidance

First, we used ANOVAs to compare the ecto-parasite burden between treatment and control nest-boxes in different age ranges of the chicks. Second, we performed generalized linear models (GLMs) on the egg-laying date, the clutch size, and the ratio of fledged eggs, where the ecto-parasite burden per nest-box (count data) was included as explanatory variable. We used AICc (Akaike Information Criterion adjusted for small sample size) instead of AIC for model comparison (Burnham and Anderson 2002). We present the full model including the following variables: ecto-parasite infestation and parent age for the egg-laying date; and ecto-parasite infestation and laying date t for other breeding parameters. We did not test for effects of the treatment (cleaned vs. un-cleaned nest-boxes) and the ecto-parasite count in the same model, due to the high correlation of both variables.

All statistical analyses were performed with the software R version 3.0.2 (R Development Core Team 2013).

3. Results

3.1. Prey remains as cue for public information

There were no significant differences in occupancy ($n = 780$) between cleaned and un-cleaned nest-boxes over the 11-year study period (51.2% un-cleaned boxes left unused vs. 56.2% un-cleaned boxes occupied; non significant results not shown). Between 2003 and 2013 the mean egg-laying date (known for a total of 337 nests) was significantly earlier in un-cleaned control

nest-boxes than in cleaned treatment nest-boxes (Fig. 1, Table 1). An earlier egg-laying date in un-cleaned control nest-boxes was consistent for each year separately, apart from 2008 and 2010 (supplementary material).

Table 1. Breeding data were analysed with generalized linear mixed models (GLMM) and the appropriate error structure. We used treatment (prey remains un-cleaned or cleaned) with different sets of covariates in a stepwise backwards model selection as predictor on egg-laying date, clutch size, ratio of fledged eggs and fledged brood size (all breeding-pairs of known age included, $n = 194$); study year and nest-box were included as random effects. For further details see statistic section in methods.

Egg-laying date	Estimate	SE	t-value	Pr(> t)	Sign.
Prey remains un-cleaned	3.92	6.03	0.65	0.516	NS
Prey remains un-cleaned x vole spring t^{\dagger}	-11.84	3.47	-3.41	0.005	**
Prey remains un-cleaned x male age (+1 year)	-7.41	4.14	-1.79	0.075	•
Prey remains un-cleaned x female age (+1 year)	-9.59	2.07	-4.64	< 0.001	***
(Intercept	53.35	3.99	13.37	< 0.001	***)
Clutch size	Estimate	SE	z-value	Pr(> z)	Sign.
Prey remains un-cleaned	0.02	0.05	0.29	0.771	NS
Fledged $t-1$	0.00	0.02	0.21	0.836	NS
Laying date t^{\ddagger}	-0.01	0.00	-2.38	0.017	*
Vole spring t^{\dagger}	0.23	0.08	2.83	0.005	**
(Intercept	1.53	0.13	12.17	< 0.001	***)
Ratio of fledged eggs	Estimate	SE	z-value	Pr(> z)	Sign.
Prey remains un-cleaned	-0.03	0.10	-0.26	0.797	NS
Fledged $t-1$	-0.02	0.04	-0.64	0.525	NS
Laying date t^{\ddagger}	-0.03	0.01	-5.40	< 0.001	***
(Intercept	0.66	0.22	3.06	0.002	**)
Fledged brood size	Estimate	SE	z-value	Pr(> z)	Sign.
Prey remains un-cleaned	-0.04	0.06	-0.67	0.503	NS
Fledged $t-1$	-0.02	0.02	-0.71	0.480	NS
Laying date t^{\ddagger}	-0.02	0.00	-4.05	< 0.001	***
Vole spring t^{\dagger}	0.34	0.10	3.48	0.001	***
(Intercept	1.35	0.14	9.38	< 0.001	***)

Note: \dagger \log_e transformed; \ddagger data presented as residuals with the study year; significance levels: '***' 0.001, '**' 0.01, '*' 0.05, '•' 0.1, 'NS' not significant.

In the global model (Table 1), the interaction term between treatment and spring vole index and between treatment and female age were significant. The interaction between treatment and male age showed a trend in predicting the egg-laying date: in years of high vole abundance egg-laying was consistently earlier and also earlier in un-cleaned nest-boxes than in cleaned ones. Older females (+1 year) initiated egg-laying earlier than yearling females, and significantly earlier in un-cleaned nest-boxes than in cleaned ones. The opposite was found for yearling breeding females (Fig. 2a).

Partners of older males (+1 year) started egg-laying earlier than partners of yearling males and again earlier in un-cleaned nest-boxes. The difference between cleaned and un-cleaned boxes was most pronounced in pairs with yearling males (Fig. 2b). There was no obvious difference in clutch size, brood size at fledging and the ratio of fledged eggs between un-cleaned and cleaned nest-boxes. The clutch size and fledged brood sizes were larger in early than late nests and during years of high vole abundance in spring. The ratio of fledged eggs was significantly lower in late nests (Table 1).

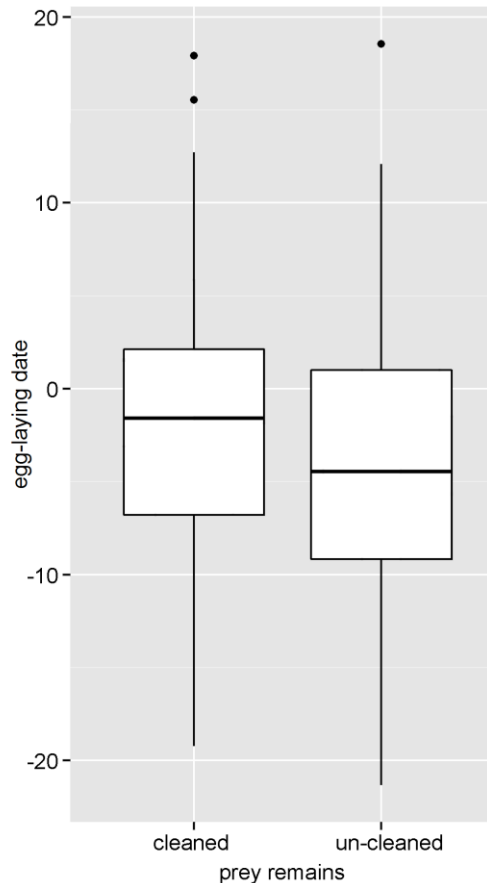


Fig 1. Mean (\pm SD, $n = 194$) egg-laying date (shown as residuals within the study year) in treatment (prey remains cleaned) and control (prey remains un-cleaned) nest-boxes. Statistical analyses can be found in Table 1.

3.2. Ecto-parasite infestation

Prevalence of ecto-parasites (*Carnus haemapterus*) was high with 237 of 259 nests (91.5%) with chicks having at least one ecto-parasite on their body. Mean number of *C. haemapterus* per nestling per nest was 10.34 ± 12.37 , and, in younger nestlings (age range 6-15 days), significantly higher in un-cleaned control broods than in cleaned treatment nest-boxes (Fig. 3). We found a weak indication for earlier egg-laying dates in higher ecto-parasite infested (un-cleaned) nest-boxes (GLM Table 2). There was no obvious effect of the ecto-parasite burden per nest-box on

the clutch size and the number of fledged eggs (GLM not significant for the ecto-parasite infestation).

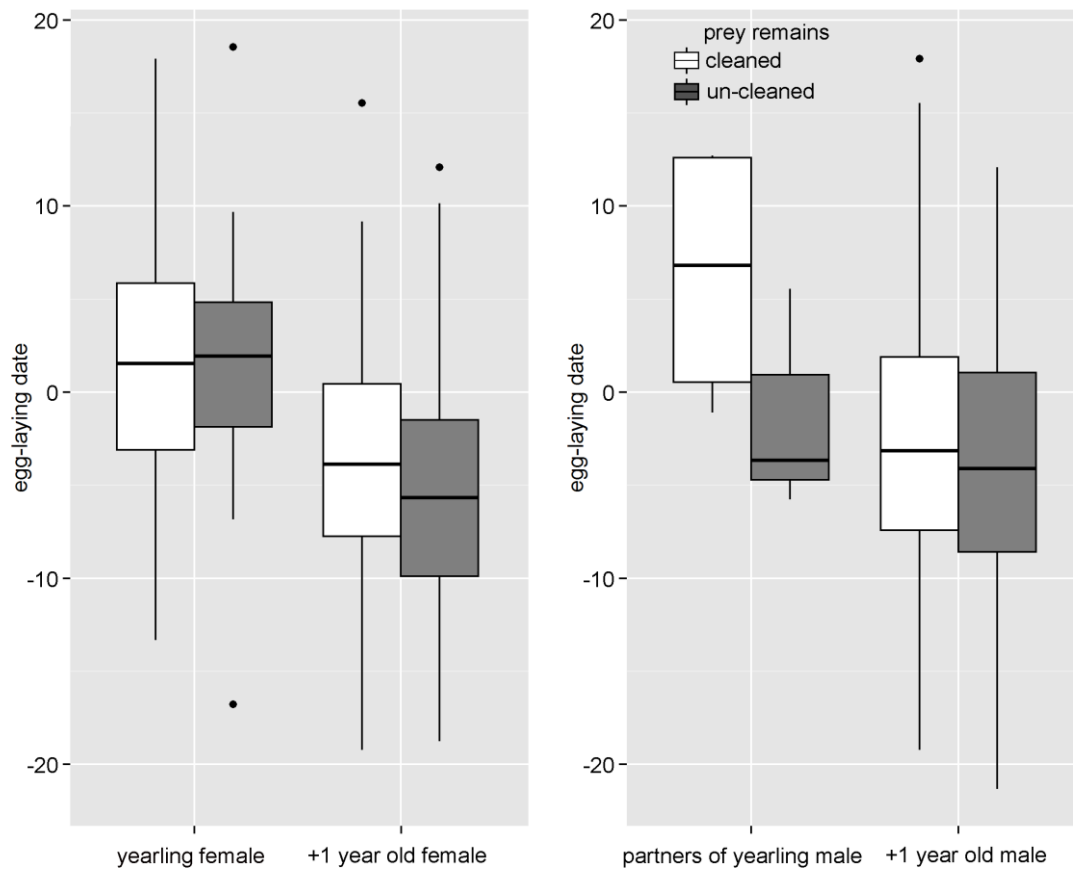


Fig 2. Mean (\pm SD, $n = 194$) egg-laying date (shown as residuals within the study year) in treatment (prey remains cleaned; white columns) and control (prey remains un-cleaned; grey columns) nest-boxes in relation to the age of the breeding male (a: left panel) and the breeding female b: right panel). Statistical analyses can be found in Table 1.

Table 2. GLM of ecto-parasite infestation (mean number of *Carnus hemapterus* per nest box) as predictor on the egg-laying date, the clutch size and the ratio of fledged eggs in 2012 ($n = 57$).

Egg-laying date	Estimate	SE	<i>t</i> -value	<i>Pr</i> (> <i>t</i>)	Sign.
Ecto-parasite infestation	-0.16	0.09	-1.73	0.089	•
Female age (+1 year)	-3.46	1.73	-2.00	0.050	*
Male age (+1 year)	-1.89	3.41	-0.56	0.581	NS
(Intercept	38.73	3.32	11.66	<0.001	***)
Clutch size	Estimate	SE	<i>z</i> -value	<i>Pr</i> (> <i>z</i>)	Sign.
Ecto-parasite infestation	0.00	0.01	0.09	0.927	NS
Laying date $t \pm$	-0.01	0.01	-1.57	0.117	NS
(Intercept	2.05	0.20	10.10	< 0.001	***)
Ratio of fledged eggs	Estimate	SE	<i>z</i> -value	<i>Pr</i> (> <i>z</i>)	Sign.
Ecto-parasite infestation	-0.03	0.03	-1.10	0.271	NS
Laying date $t \pm$	-0.02	0.03	-0.64	0.520	NS
(Intercept	2.58	1.25	2.07	0.039	*)
Fledged brood size	Estimate	SE	<i>z</i> -value	<i>Pr</i> (> <i>z</i>)	Sign.

Ecto-parasite infestation	-0.01	0.01	-1.20	0.231	NS
Laying date $t \pm$	-0.01	0.01	-1.68	0.093	•
(Intercept	2.00	0.23	8.70	< 0.001	***)

Note: significance levels: '***' 0.001, '**' 0.01, '*' 0.05, 'NS' not significant.

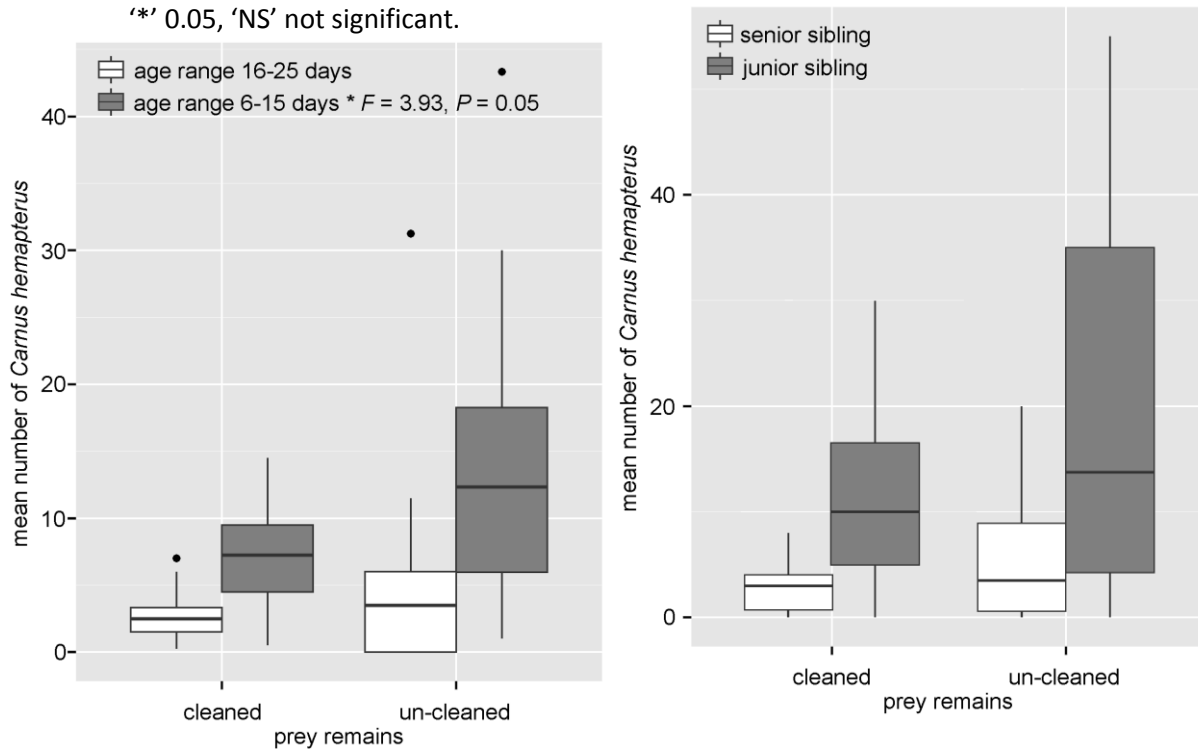


Fig. 3. Mean (\pm SD) number of *Carnus hemapterus* on the host in relation to the age of nestlings. Left panel: only 2nd ranked chicks at the age of 6-15 and 16-25 days (grey and white columns, respectively); right panel: junior (last-hatched chick, grey columns) and senior (first-hatched chick, white columns) siblings in cleaned ($n = 32$) and un-cleaned ($n = 57$) broods in 2012. Stars denote statistically significant differences in a one-way ANOVA between cleaned and un-cleaned nest-boxes (count data transformed by logarithm function).

4. Discussion

Two main results emerged in our study. First, the presence or absence of prey remains of the previous breeding season in nest-boxes had a significant influence on the egg-laying date, which was earlier in un-cleaned than cleaned boxes. This indicates that prey remains revealed a successful breeding attempt in the box, and are therefore used as public information in the settlement decisions of kestrels. Second, the ecto-parasite burden of younger nestlings (age 6-15 days) was higher in un-cleaned control broods than in cleaned nest-boxes, but the ecto-parasite infestation had no obvious effect on breeding success.

4.1. Public information and breeding performance

Our results support the use of public information as an important mechanism in nest-site choice of the studied kestrel population. Information seems to be transferred between unrelated conspecifics by using a layer of prey remains as an indirect cue for previous breeding success. There was advancement in egg-laying date which could be explained by the presence of prey remains

in control nest-boxes. Earlier initiation of egg-laying in un-cleaned than cleaned boxes indicates that nest-boxes with prey remains are selected first by kestrels. Laying order of kestrel populations is closely correlated with arrival dates from spring migration. Early arriving males attract a mate first, and these pairs start egg-laying earlier than late arriving conspecifics (Palokangas et al. 1992; Village 1985). Earlier arriving individuals are usually of higher individual quality (older, larger and in better body condition) than later arriving ones, and settle on progressively lower quality territories ('sequential settlement', see Sergio et al. 2007). Early arrival has therefore reproductive consequences.

The treatment had a stronger effect on clutch initiation than the actual number of fledged young in the previous year of the site. Furthermore, the vole index in previous autumn had no obvious effect on tested breeding parameters, indicating that kestrels do not use vole abundances of the previous year in their settlement decisions either. We alternatively included the egg-laying date of the previous year (laying date $t-1$) to test for individual differences of the nest-site, without having any explanatory capacity (both models not shown).

We found a significant influence of the age of the breeding parents on the egg-laying date, in addition with the treatment and the vole index in spring of settlement (Table 1). The crucial role of the male parent in determining the start of egg-laying is not unexpected, because it is the male that occupies the nest-box first (who can actually use prey remains as a cue for previous breeding success at the site chosen), and provides most of the food to the female during pair formation, courtship feeding and egg-laying periods (Korpimäki and Wiehn 1998; Tolonen and Korpimäki 1994; Village 1990). According to our results, partners of yearling males started egg-laying later in the season than partners of older males. The influence of age or breeding experience on clutch initiation and reproductive success is well known (Forslund and Pärt 1995; Limmer and Becker 2007; Riechert et al. 2012), also in raptors (Espie et al. 2000; Palokangas et al. 1992). Generally young breeders show lower breeding success than old breeders, although a longer breeding experience turned out to be more important for success than age per se (Angelier et al. 2007). In raptors, male quality is particularly important, as males have the sole responsibility for prey delivering during early nesting, and experienced males have usually higher foraging success.

For breeding females we found a significant interaction between earlier egg-laying in un-cleaned nest-boxes. But this was only found in older breeding females (+1 year), while yearling breeders showed the contrary. An earlier egg-laying in cleaned boxes in yearling breeding females could be due to a general low percentage of individuals breeding already in their 2nd calendar year. We assume that young females are mating with males of low individual quality and are occupying accordingly breeding sites of seemingly low habitat quality. Since pellets and other prey remains are used as an indirect cue for a 'good' nest-site, it is likely that cleaned boxes

are all that is left when yearling breeders finally start incubating. Nonetheless, control nest-boxes with prey remains left were settled first in the season, independent from the age of the breeding parents.

We found no indication that individuals that followed different strategies (reuse un-cleaned or choose cleaned nest-boxes) had differences in breeding success. Beside the laying date and the vole index in spring neither treatment nor previous number of fledged young (fledged $t-1$) at a nest-site had a significant influence on the clutch size. Moreover, the adaptation to a scarcer food supply in low vole years happens already in the clutch state (Korpimäki and Wiehn 1998), meaning that the ratio of fledged eggs was dependent on the laying date, but not on the vole abundance in spring.

One fact which needs to be taken into account is that a manipulation of cues used by kestrels during settlement does not change the 'real' habitat quality around the nest-box. Therefore, we might have some good breeding sites that may appear of lower quality due to the experiment we conducted and respectively some bad breeding sites that appear of higher quality. We reduced such possible effects by the randomisation of the cleaning procedure and by exclusively analysing nest-boxes which has been successful in the previous year. Nonetheless, the treatment does not manipulate habitat quality. This might explain that cleaned boxes, generally occupied later in the breeding season, still revealed a comparable breeding success to un-cleaned nest-boxes. Seemingly less attractive breeding sites (treatment) may still be surrounded by foraging areas of high quality, which might also depend on the phase of the vole cycle. For example, more diversified alternative prey communities or more locally stable vole populations could be a guarantee of high breeding success even during poor vole abundance years.

4.2. Ecto-parasite avoidance hypothesis

Ecto-parasite burden was higher in un-cleaned control nest-boxes than in cleaned ones, at least in the early stage of the nestling phase (chick age 6-15 days), whereas un-cleaned boxes with higher ecto-parasite infestations were settled earlier in the breeding season. Parasite-induced adaptations usually occur during parasite exposure, e.g. in an alteration of the start of reproduction (Oppliger et al. 1994), of the clutch size (Martin et al. 2001; Møller et al. 1997; Richner and Tripet 1999), or also of parental investment (Christe et al. 1996; Fitze et al. 2004; Tripet and Richner 1997). In our study we found the opposite correlation for the laying date. Since ecto-parasite burdens were higher in un-cleaned control nest-boxes, we have to consider again the value of prey remains as a cue for a 'good' breeding site. Models of habitat selection suggest that animals settle first in sites of highest quality and once these sites are filled, offspring produced locally and individuals immigrating from elsewhere are forced to settle in sites of lesser quality (Fretwell and Lucas 1969). If un-cleaned nest-boxes are preferred, we can assume that breeding pairs with higher individual quality are breeding earlier in the season in un-cleaned nest-boxes

and producing larger clutches despite the higher ecto-parasite burden. Further, there was no significant difference in clutch size, ratio of fledged eggs and fledged brood sizes related to the ecto-parasite infestation of the nest-box. Contrary to our results, brood size at hatching of great tits was significantly smaller in infested nests than in parasite-free nests (Oppliger et al. 1994). In Bonelli's eagles (*Hieraaetus fasciatus*) the use of multiple nests, simultaneously with the presence of greenery as mechanisms for cleaning ecto-parasites, was an important factor for the breeding success (Ontiveros et al. 2008). This suggests that the reduction of nest ecto-parasites is a plausible explanation for the maintenance of alternative nests in raptor species constructing nests themselves. Comparability of these findings is limited, however, since falcons are not able to build a nest, but use stick-nests or other structures to breed. Therefore, a completely parasite-free nest is hard to find. If ecto-parasite avoidance is occurring in the settlement decisions of kestrels it seems to be strongly limited by supply and demand.

Conclusions

The use of prey remains revealing successful breeding attempt in the previous year as public information appeared to be important in the settlement decision of kestrels, since they started egg-laying earlier in un-cleaned control than in cleaned treatment nest-boxes. On the other hand, there was no strong evidence for nest-box reuse being advantageous since fledged brood sizes remained equal in control and treatment nest-boxes. Our data do not lend support to the ecto-parasite avoidance hypothesis, since un-cleaned nest-boxes with higher ecto-parasite infestation were settled earlier in the season than cleaned ones.

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Ethical standards

All experiments and sampling was conducted in strict accordance with current Finnish and EU law and followed the Weatherall Report and the guidelines for the treatment of animals in behavioural research and teaching (ASAB 2012).

5. References

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Supplementary material 1: mean egg-laying date (\pm SD) in cleaned treatment nest-boxes and un-cleaned control nest-boxes between 2003 and 2013; egg-laying date earlier in control broods (+) or earlier in treatment broods (-).

Study year	Vole cycle phase	N	Cleaned boxes		Un-cleaned boxes		
			Mean (\pm SD)	Earliest date	Mean (\pm SD)	Earliest date	
2013	low	31	May 13 (\pm 6.8)	May 6	May 11 (\pm 5.5)	May 2	(+)
2012	decrease	53	May 6 (\pm 8.9)	April 24	May 3 (\pm 8.2)	April 18	(+)
2011	increase	13	May 8 (\pm 12.4)	April 25	May 1 (\pm 13.5)	April 20	(+)
2010	low	25	May 10 (\pm 6.7)	May 1	May 13 (\pm 11.2)	May 2	(-)
2009	decrease	59	May 2 (\pm 8.9)	April 19	April 28 (\pm 5.9)	April 19	(+)
2008	increase	34	May 1 (\pm 6.5)	April 17	May 3 (\pm 5.7)	April 25	(-)
2007	low	22	May 15 (\pm 7.6)	May 2	May 13 (\pm 7.2)	May 2	(+)
2006	decrease	37	May 5 (\pm 5.0)	April 26	May 3 (\pm 4.0)	April 28	(+)
2005	increase	22	April 29 (\pm 6.4)	April 17	April 23 (\pm 10.6)	April 14	(+)
2004	low	13	May 7 (\pm 9.5)	April 28	May 3 (\pm 3.5)	April 27	(+)
2003	decrease	28	May 10 (\pm 9.4)	April 30	May 6 (\pm 9.3)	April 23	(+)

Supplementary material 2: Nestlings in cleaned nest-boxes($n = 32$) and control broods (prey remains left, $n = 57$) in 2012 and *Carnus hemapterus* burden at 1-15 days old chicks and 16-25 days old chicks as well as parasite burden of the first and last chick hatched; one-way ANOVA.

Variable	Treatment brood	Control brood	<i>F</i>	<i>P</i>	Significance
<i>C. hemapterus</i> [†] per nestling					
age 1-15 days	7.9 ± 7.0	14.2 ± 12.2	3.93	0.051	•
age 16-25 days	2.5 ± 2.7	5.6 ± 9.4	2.50	0.118	NS
first (senior) chick hatched	2.9 ± 2.6	5.8 ± 6.5	1.87	0.175	NS
last (junior) chick hatched	11.0 ± 7.8	19.2 ± 17.7	0.50	0.481	NS
Body mass/wing length (g/mm) †	1.59 ± 0.29	1.61 ± 0.25	1.02	0.314	NS

Note: † Log_e transformed

Significance codes: '•' 0.1, NS not significant.

4. Concluding Discussion

4.1. City slickers

The Vienna Kestrel Project was initiated in 2010 with the aim of elucidating the reasons for the Eurasian kestrel's apparent success in the city. As a result of the findings, our understanding of the species' performance in the city has changed and it appears that historic buildings in the city centre might represent ecological traps for kestrels. This represents a paradigm shift in our way of thinking about the kestrel. A three-year period is too short to generate sufficient data on the viability of the population to state conclusively whether the classic Robertson and Hutto (2006) definition applies, according to which an ecological trap is a behavioural rather than a population phenomenon. Nevertheless, I am able to hypothesize that kestrels in Vienna prefer to colonize a lower-quality habitat despite the availability of better options. Further work will be required to test this hypothesis.

At the start of the work it seemed highly likely that the kestrel had one or more strategies to enable it to succeed in the city centre. In a pilot study in 2009 I recorded the highest population density documented to date in a non-colonial breeding population in a European city. With 250-400 breeding pairs (Wichmann et al. 2009), the kestrel occurs in Vienna at a higher density than in e.g. Berlin (Kübler et al. 2005) and Paris (Malher et al. 2010) and the concentration is even than that found in rural areas (Gamauf 1991; Mebs and Schmidt 2006). Nevertheless, further analysis clearly demanded that I question the paradigm that breeding occurrence and abundance can be equated to suitability of habitat. My PhD project was thus conceived as a cost/benefit analysis.

4.2. The benefits of urban breeding

The results presented in **Chapters I and II** reflect the high abundance of breeding kestrels in the city centre, as indicated by shorter nearest-neighbour distances (Chapter I: Fig. 1, 2). Within highly populated areas I found that kestrels show a preference for roof-openings and nest sites on buildings in the vicinity of green courtyards (Chapter I: Table 1; Chapter II: Fig. 2).

The breeding occurrence of falcons is limited by the availability of potential nest sites (Newton 1979; Village 1983). A significant correlation between the number of nests and the number of roof-openings supports the notion that more kestrels breed in the centre due to the greater availability of cavities resulting from the historic building structure. The cavities have a number of attributes generally associated with higher breeding success, such as inaccessibility to predators, protection from rain and sun and a low likelihood of collapse (Charter et al. 2007b; López et al. 2010). The outskirts lack historic buildings with roof-openings; here kestrels depend on

the availability of stick-nests or resort to nesting in window boxes. The nearest-neighbour distances increase as a consequence of the limited number of preferred nest sites.

4.2.1. The use of prey remains as (misleading) public information

Kestrels clearly seem to prefer breeding in cavities than in open nests (see **Chapter II**). It is possible that they use 'public information' in making their choice. Building cavities in the urban study system are loaded with pellets and prey remains, which could be an indirect indication of the presence of conspecifics and of past reproductive success. Public information may even be more important than habitat features in selecting nest site (Aparicio et al. 2007; Hoi et al. 2012). By means of an experimental set-up we showed that un-cleaned nest boxes were preferred over cleaned ones, independent of previous breeding success at a site (**Chapter VI**). The abundance of previously occupied breeding cavities may be a further reason for kestrels to breed in the city centre. In support of this notion, kestrels were found to reuse the same building cavity over many years (data not shown). The structural element of roof-openings offers a high number of cavities with the exact same size, height and direction in a single building (unpubl. data). Nevertheless, kestrels reuse the same cavity for many years. The 'public information hypothesis' would predict an earlier laying date in these seemingly high quality habitats in the centre, unless the shorter nearest-neighbour-distances result in higher competition and higher aggression between neighboring pairs (pers. obs.), which might delay the onset of breeding.

4.2.2. Sequential settlement

Intraspecific competition limits the access to ideal nest sites (Chalfoun and Schmidt 2012). Models of habitat selection suggest that animals settle first in sites of highest quality ('ideal free' or Fretwell-Lucas Model, Fretwell and Lucas 1969). For territorial birds such as the kestrel the model predicts a sort of ideal-despotic distribution (Fretwell 1972) in which the fittest males preferentially occupy the best sites and poorer sites are occupied by less competitive individuals, resulting in site-dependent breeding success. Sites settled last are usually lowest in quality and potentially function as habitat sinks (Pulliam and Danielson 1991). Under normal circumstances, one would expect the territories occupied first to show the highest breeding success but our study revealed the opposite to be the case. The times of arrival at the nest site of kestrels breeding in Vienna showed that inner-city birds tended to arrive earlier than their suburban conspecifics (Chapter I: Table 2a), suggesting that inner-city sites are perceived as being of the highest quality. However, there were no differences in laying dates along the urban gradient and breeding performance (Chapter I: Table 2b) was worse in inner-city districts than in the outskirts. Thus, the first returning kestrels do not select the best breeding sites.

This finding is in direct contradiction to the predictions of the Fretwell-Lucas Model. Possible explanations for the discrepancy are discussed in **Chapter I**. They include (i) an annual invasion

of urban Vienna due to population pressure from rural kestrel populations at capacity level and/or (ii) a lower availability of nest sites in rural areas. If the former explanation were true, arrival times in the city centre should be later than arrival times in the suburbs but this did not appear to be the case. Support for the latter explanation is provided by the evidence (see **Chapter II**) that the kestrel prefers nesting in cavities in buildings, a structural feature that is absent from the outskirts of the city. Further possible explanations for the annual invasion of the city are linked to the abundance of prey. Kestrels might respond (iii) to the perceived higher abundance of prey in the city or (iv) to the perceived lower abundance of prey in rural areas. These possibilities are easy to discount. I found small rodents to be equally distributed in all urban areas examined, although the rodents in the city centre are almost exclusively nocturnal and thus unavailable to diurnal raptors (Chapter I, results). Nevertheless, there was a high abundance of prey-sized species of bird in urban parks and green backyards (Chapter II: Fig. 3), with individual species present in numbers comparable with those in the outskirts (gardens and forests).

4.2.3. Young breeders and floaters

A study of the goshawk (*Accipiter gentilis*) in the city of Hamburg, Germany, revealed that a large proportion of breeding recruits were young birds in their first or second calendar year (Rutz 2008). Analysis of breeding success in populations with a large proportion of young birds is complicated by the fact that it is expected to be lower in young breeders (e.g. Laaksonen et al. 2004) and to increase in more experienced individuals. In my urban study system, the kestrel nestlings were banded with two different rings, one from the Radolfzell Ringing Center, Germany and an electronically coded PIT ring. The latter (TIPES ring MC 601) allowed a quick recognition of individuals in the following years by means of an electronic scanning device inserted into the nest cavity, avoiding time-consuming direct reading of rings. No young breeder in its second calendar year was registered in the urban study area via the electronic rings (unpublished data 2011-2012). Furthermore, I did not observe any young breeding kestrels in the study area. I conclude that the observed differences in breeding success were not due to inexperienced individuals.

The apparent discrepancy between my results and those of Rutz (2008) stems from the fact that the goshawk population in Hamburg is relatively young and still at the stage of expansion, whereas the kestrel population in Vienna is well established and stable (Wichmann et al. 2009). It is known that many raptor populations are at full capacity, so some sexually mature individuals are unable to breed because all suitable nest sites are occupied. Such 'floaters' typically remain in the area and wait for a breeding site to become available (Kenward et al. 2000; Kokko et

al. 2004; Rutz and Bijlsma 2006; Tanferna et al. 2013). This is presumably the case for the kestrel population in Vienna.

4.3. The costs of urban breeding

The kestrel population in Vienna seems to be at full capacity, with the kestrels that breed in the centre of Vienna benefiting from the ready availability of suitable nest sites, particularly cavities in the historic buildings. If breeding in the inner city is to be as successful as breeding in rural areas, the higher density of kestrels in the city centre should be accompanied by a greater availability of sufficient prey. Is this actually the case? This question may only be investigated by means of a reliable method to analyse what prey kestrels take in different breeding sites.

4.3.1. Diet studies of raptors: methods and applications

The traditional method of investigating diet relies on an analysis of remains in pellets but the results may give an incomplete picture because raptors have far more efficient digestive systems than owls and many items of prey cannot be detected in pellets. Vertebrate bones and invertebrate prey such as grasshoppers and butterflies cannot be satisfactorily identified by analysing pellets and this makes a quantitative assessment of the diet composition extremely difficult. Direct monitoring of the nest site might be more accurate but studying the footage obtained by video monitoring is even more time consuming than analysing pellets. Video monitoring is associated with technical limitations and because of the cost of the equipment it cannot be used to study as many nests as can be investigated by pellet analysis. Nevertheless, both approaches can contribute valuable information and I used both of them in the project.

In **Chapters I** and **III** I used pellet analysis to acquire a larger sample size to compare diet choice between the three urban zones. Despite the use of this 'large-scale' method the number of nest sites investigated was too small to permit a detailed statistical analysis of diet choice along the gradient of urban habitat. The work in **Chapter II** I address the importance of avian prey, for which a very precise measurement of the avian prey ratio was essential. I thus selected video monitoring as the more suitable and accurate method.

4.3.2. The mismatch between the abundance and availability of prey and the resulting diet choice

Surprisingly, the higher density of kestrels in the city centre is not accompanied by a greater availability of sufficient prey. My data clearly indicate a trade-off between the ready availability of breeding cavities and the greater distances to hunting grounds. The trade-off results in a shift in the main prey taken by kestrels in the centre. The high density of kestrels breeding in sealed urban areas is linked to significantly lower breeding success, suggesting that there is insufficient

prey available in the city centre despite the abundance of *Apodemus* rodents. Pellet analysis found that kestrels breeding in urban areas feed on *Microtus* voles and only rarely catch the abundant but unavailable *Apodemus* species (**Chapter III**). Urban kestrels are thus forced to fly longer distances to rural hunting grounds or to switch to types of prey that are available in the city.

Although raptors have large home ranges that can extend beyond urban boundaries (Chace and Walsh 2006; Riegert et al. 2007a; Riegert et al. 2007b), the increasing proportion of alternative prey in the diet of kestrels along the gradient from the suburban area to the centre indicates that Viennese kestrels prefer to hunt in the immediate surroundings of their breeding sites. They rely on food sources available within the urban setting and as predicted shift from feeding largely on rodents to consuming more passerines and even occasionally larger birds such as feral pigeons. The kestrel's diet in the city centre and in the mixed zone is very diverse (higher Levin's index), indicating that although their suburban and rural counterparts are specialized in hunting voles urban kestrels are generalists. Crucial to understanding diet choice is the finding that abundance of prey cannot be equated to availability of prey. This point is underlined by the results in Part 1. The choice of method to analyse diet choice is thus extremely important.

4.3.3. Predicting availability of prey

It may be difficult for kestrels at the stage of habitat selection to evaluate the availability of food during the future breeding period (see Hollander et al. 2013; Török et al. 2004 and citations therein). Kestrels have been shown to use ultraviolet vision and UV-reflecting rodent scent marks to identify suitable hunting areas (Viitala et al. 1995, but see also Lind et al. 2013). Because rodents are abundant in the city centre, there should be a large number of scent markings and the kestrels are presumably unable to tell that the majority of the rodents that cause them are nocturnal and therefore do not represent potential prey. Other possibly misleading cues are the high availability of passerines as alternative prey, although they are thought to be harder for kestrels to catch, and the presence of a large number of conspecifics, which could be expected to be indicative of good hunting areas (Fletcher 2006; Hromada et al. 2008).

The misleading cues may well lead to mistakes in the assessment of food resources, potentially inducing a mismatch between habitat preference and habitat quality (Hollander et al. 2013; Kloskowski 2012). As a consequence, the kestrels preferentially settle in low-quality habitats despite the availability of better options. This is a type of maladaptive behaviour that causes the species to fall into what is known as an ecological trap (reviewed in Battin 2004; Kokko and Sutherland 2001; Kristan 2003; Robertson and Hutto 2006; Schlaepfer et al. 2002).

4.3.4. Ecological traps and habitat sinks

Radio-tracking studies on urban kestrels have shown that city populations fly longer distances to their hunting grounds (Riegert et al. 2007a; Riegert et al. 2007b). Nevertheless, urban areas are chosen for nesting. The apparent paradox has been explained by the possibility that the number of nest sites in the surroundings are severely limited nest, or by proposing that the quality of habitat in the centre is higher, possibly connected to lower predation risk in the centre. Neither of these theories was supported by my study. The city of Vienna is of lower habitat quality – in terms both of prey availability and of reproduction success – than the surrounding areas.

To interpret the results, it is important to distinguish between ecological traps and habitat sinks (see Kristan 2003). An ecological trap may have no consequences at the level of the population (Robertson and Hutto 2006). If the animals in the ecological trap encounter severe problems and the resident population is not self-sustaining, the area is instead defined as a habitat sink (Donovan and Thompson 2001). In accordance with this definition, my findings of lower reproductive performance indicate that urban kestrels are falling into an ecological trap in the centre of Vienna. Proof of a habitat sink would require the demonstration that productivity in the urban area is insufficient to offset mortality (Pulliam 1988). Unfortunately, a study period of three years is too short to reveal a decline in the urban population.

Other components of fitness should also be considered, such as the rate of recruitment of juveniles into the breeding population and the survival of the adults). Dispersal from adjacent areas might also be important and it is conceivable that the urban population is only sustainable through immigration from suburban and rural areas. The high mortality of nestlings of Cooper's hawk (*Accipiter cooperii*) in Tucson, Arizona from trichomoniasis has prompted speculation that the urban area represents an ecological trap (Gilroy and Sutherland 2007), but a long-term study of annual survival rates showed them to be relatively high, especially of juvenile hawks, and this was inconsistent with the idea of a habitat sink (Mannan et al. 2008). I plan in the future to address recruitment, turnover rates and adult survival. The work will be facilitated by the fact that during the present study all nestlings and some of the breeding adults have been ringed with electronic PIT rings. The rings will help us to collect additional data from which we shall be able to calculate the local rate of recruitment and the survival rate.

4.4. Reduced reproductive rate and sex-biased nestling survival

It is known that malnutrition is the main cause of mortality for urban nestlings of the lesser kestrel and it has been linked to difficulties in finding food (Tella et al. 1996). For Montagu's harrier (*Circus pygargus*), it has been shown that the mortality of nestlings is sex-biased, with a higher probability of death for smaller males, especially if they hatch later in the season (Arroyo 2002).

There have been some indications of a biased sex ratio in urban kestrels: Rejt et al. (2005) report that pairs in the centre Warsaw had more female offspring and that female chicks hatched earlier than their brothers.

In Viennese kestrels, the youngest chicks in a nest and the smaller males were most likely to die as nestlings, suggesting that starvation is the main reason for the lowered survival rate (**Chapter I**). The preferential survival of female chicks led to a shift from the initial 1:1 sex-ratio after hatching to a surplus of female fledglings. I also observed that the larger sex predominated in the earliest chicks to hatch. There have been reports of a seasonal trend in the sex ratio of kestrel chicks, with progressively more female offspring and a decline in clutch size for later laying dates (Dijkstra et al. 1990b). My study was consistent with this finding: later nests in the centre produced more females and smaller fledged broods. It has previously been noted that late broods are typically produced under circumstances when less food is available and that the parents have less time to feed the young before they must migrate or disperse. The mortality in such broods is higher, both before and after fledging (Dijkstra et al. 1990a). My findings go beyond the earlier work in that they show that the shift from a male bias in early nests to a female bias in later nests is not due to a change in the primary sex-ratio but to sex-specific survival of chicks in the nests in the centre of the city. I have collected a considerable amount of data in an attempt to unravel the factors that determine that condition of the young and thus their chances of survival. Analysis is still at a fairly preliminary stage but there are indications that the higher level of infestation with ectoparasite in breeding cavities than in open nests may be one of the factors behind the lower rate of survival of nestlings in the city centre.

4.5. The 'tasty chick' hypothesis

I investigated the effect of ectoparasite infestations in the Finnish kestrel population, where I found an accumulation of ectoparasites on the final chick to hatch (the junior sibling).

In many altricial bird species, weight hierarchies of nestlings within broods are the result of hatching asynchrony, induced by starting incubation before the completion of the clutch. The 'tasty chick' hypothesis (Christe et al. 1998; Roulin et al. 2003) proposes that hatching asynchrony has evolved as an anti-parasite strategy. The poor body condition of the later chicks impairs parasite resistance and makes them particularly vulnerable to ectoparasites. Parasites may preferentially feed on the less immune-competent nestlings within a brood: from a parasites' point of view, the 'tasty chick'. Hosts also benefit from collecting ectoparasites on the offspring with the lowest reproductive value within a brood, i.e. on the final chicks to hatch. In effect, the final offspring are sacrificed to the parasite. The behaviour could be adaptive if the overall reproductive success of a breeding pair is increased by permitting the cost of parasitism to be carried by the junior nestlings of a brood, thereby preventing complete nest failure.

The work described in **Chapter VI** enabled us to confirm one prediction of the tasty chick hypothesis, finding that the last chicks to hatch showed significantly higher rates of infestation with ectoparasites than their senior siblings. Nevertheless, the higher rates of infestation did not have any obvious effect on the average body condition of the fledglings nor on the overall breeding success of the pairs (Chapter VI: supplementary Material 2). The findings need further evaluation and a comparison to the study system in Vienna might be revealing.

5. References

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With four supervisors one can imagine how easy it would be to get lost between all the different institutions, but everything depends on the people you have the pleasure to work with. I found myself in an amazing team at the Natural History Museum, where I could move between the bird collection, the genetic lab and also the mammal collection, depending on what was needed: an actual working space, advice, a coffee or a glass of sparkling wine. I cannot list everybody, so I will just name Elisabeth Haring, Barbara Däubl and Frank Zachos. Thank you all, for making the museum such a nice and inspiring place to work.

Compared to the Museum I have spent little time at the former department of evolutionary biology and nowadays the integrative zoology, but I always felt very much welcome. Thank you for helping me out whenever needed: Hannes Paulus and Andreas Wanninger for financial support of my project, Anita Morth for taking such good care of my project accounting, Eva and Johannes for advice in the lab, Norbert for statistical advice, and all the friends who came together for one or another beer on the terrace: Flo, Linde, Nora, Julia, Kerstin, Martin, Joseph, Andi and Barbara. A special thanks goes to my birding friends with whom I have spent many days and wonderful moments enjoying nature in Hohenau, Marchegg, Illmitz, Helgoland and of course at BirdLife meetings. You have been great de-stressors by dragging me outside the city.

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Vienna, 05. Mai 2014

Curriculum Vitae

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Academic Formation

- Since 2014 **Post-Doctoral Fellowship 2014**
at the Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, South Africa
- 2009-2014 **Ph.D. in Zoology (Dr. rer. nat.)**
Department of Integrative Zoology, University of Vienna: supervised by Prof.
Harald W. Krenn, in collaboration with the Natural History Museum Vienna, Prof.
Anita Gamauf and the University of Turku, Finland, Prof. Erkki Korpimäki
- 2009 Degree in environmental education (World Wide Fund for Nature, Austria)
02. 04. 2009 **Mag.rer.nat.** – thesis with excellent success (grade 1)
- 2004-2009 Biology and Environmental Studies and French (Secondary School Teacher
Accreditation Programme) University of Vienna, Department of Evolutionary
Biology
21. 06. 2002 **Matura** with excellent success (grade 1)
- 1994-2002 Bundesrealgymnasium Klagenfurt-Viktring, Austria

Professional experience, Field assistances and Workshops attendances (selection)

- 2014 Spring School in Landscape Genetics, University of Göttingen, Germany
- 2008-2012 Assistant at the Bird Ringing Center in Hohenau, Austria
- 2007-2012 Keeper and falconer at raptor rescue station, Burg Landskron, Austria
- 2009-2011 WWF Austria, trainer in environmental education
- 2007-2011 Biology teacher at the Maturaschule Dr. Rampitsch Vienna, Austria
- 2010 Field assistance in West Java and Krakatau; Bogor Agricultural University,
Indonesia
- 2010-2011 Assistant at the Bird Ringing Center in Illmitz, Austria
- 2007-2010 Education department and guided tours at the Zoo Vienna, Austria
- 2009 Field assistance in Piedras Blancas National Park; research station La Gamba,
Costa Rica
- 2007 Field assistance in costal ecosystems of the Sinai Peninsula in Dahab, Egypt
- 2006 Work shop in Marine Biology, HYDRA Institute for Marine Biology, Elba, Italy

2006 Editorial assistant and translator for the radio station «5FM - Radio Centre Ville»
Montreal, Canada

Teaching experience

2014	Lecturer in Didactics in field biology [Freilanddidaktik in LA – BU] University of Vienna
2011-2014	Lecturer in Interdisciplinary Excursions [Interdisziplinäre Exkursionen LA – BU] University of Vienna
2011-2014	Lecturer in Zoology I and II, Ecology, Cell biology and genetics [Zugang zu den tierischen Lebewesen, Vielfalt des tierischen Lebens, Vielfalt von den Lebensräumen auf unserem Planeten, Zugang zur Zelle und ihren Bausteinen] University of Education Vienna
2008-2010	Tutor in Practical Lab course on Animal Diversity, Organization and Biology [Diversität, Organisation und Biologie der Tiere] University of Vienna

Key competencies and skills

- Broad knowledge and experience in the field of avian ecology
with particular emphasis on behavioural and urban ecology and raptor research
- Strong presentation and communication skills, with experience in teaching
at University level
- Media relations experience (broadcasting and press interviews)
- Good management and leadership skills
- Strategic planning in Foundations and Grant-Making
- Advanced computer skills in biostatistics, spacial analyses and basics in landscape genetics
- Advanced level language skills
German native, English and French excellent in reading, speaking and writing
- Work experience in DNA laboratory (2 years, sexing of birds, microsatellites)

Computer literacy: ArcGIS, R Studio, StatSoft Statistica, IBM SPSS, Estimate S, Primer, MARK, Tadem, Cervus, Colony, Genepop, Microchecker, FSTAT

Licenses: driver's license (A-motorbike, B-car, and E-trailer); tree climbing license (SKT-A); hunting and falconry license; diving license (bronze*)

Raptor Research and Management Techniques: nest-box trapping, bal-chatri trapping, direct bleeding at the brachial vein, indirect bleeding via *Dipetalogaster maximus*, attaching telemetry devices as backpack or on tail feathers, conventional telemetry

Research grants and Scholarships

Short-term grant abroad 2014 – University of Göttingen, Germany (March 2014) and University of Turku, Finland (April 2014)

Marietta Blau Grant of the OEAD 2013 – University of Turku, Finland

DOC-fORTE Grant of the Austrian Academy of Science 2011-2012

Grant of the Vienna Science and Technology Fund (H-2483/2012)

Grant of the Environmental Protection Bureau of Vienna (MA 22-2220/2010)

Doctoral Research Fellowship University of Vienna 2010

Grant of the Dr. Maria Schaumayer-Stiftung 2009

Research Scholarships, University of Vienna 2008

Performance Scholarships offered by private institutions, University of Vienna (2008)
 Performance Scholarships (StudFG) offered by the bm:bwk, University of Vienna (2006)
 Performance Scholarships offered by private institutions, University of Vienna (2006)

Conference presentations (*received Travel Awards are indicated*)

- 2014-04-03 AURA Symposium, Åbo Akademi University, Turku, Finland
 - talk and Proceedings contribution (Short-term grant abroad, University of Vienna)
- 2013-10-21 1st Worldwide Raptor Conference, Bariloche, Argentina
 – Chair person, talk, poster and Proceedings contribution
- 2013-08-28 9th Conference of the European Ornithologists' Union (EOU), Norwich, UK
 – talk and Proceedings contribution
 (Student Grant of the British Ornithologists' Union)
- 2013-04-13 Symposium: Wildlife in urban and suburban regions, Halberstadt, Germany
 – poster and published conference paper
- 2012-08-16 5th North American Ornithological Conference (NAOC), Vancouver, Canada
 – talk and Proceedings contribution
 (Student Travel Award of the NAOC-V, Dissemination University of Vienna)
- 2011-09-29 144th German Ornithologists' Society (DO-G), Potsdam, Germany
 – poster and published conference note - honoured with best poster award
 (Dissemination University of Vienna)
- 2011-08-27 8th Conference of the European Ornithologists' Union (EOU), Riga, Latvia
 – talk and Proceedings contribution
 (Student Travel Award of the German Ornithologists' Society)
- 2011-05-03 7th Ecology and Behaviour meeting (SERL), Rennes, France
 – talk and Proceedings contribution (Dissemination University of Vienna)
- 2010-10-22 Symposium: Population Ecology of Raptors and Owls, Halberstadt, Germany
 – poster and submitted conference paper
- 2010-05-28 Symposium: March-Thaya Floodplain Forests, Vienna, Austria
 – talk and published book chapter
- 2009-10-04 142th German Ornithologists' Society (DO-G), Pörschach, Austria
 – talk and published conference note

Reviewing work

Journals: Ibis (2013), Journal of Raptor Research (2012)

Publication List

Peer-reviewed journals:

1. **SUMASGUTNER, P.**, NEMETH, E., TEBB, G., KRENN, H.W., GAMAUF, A. (accepted): 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*.
2. **SUMASGUTNER, P.**, SCHULZE, C.H., KRENN, H.W., DÜESBERG, J., GAMAUF, A. (2014): Conservation related conflicts in the nest-site selection of the Eurasian Kestrel (*Falco tinnunculus*) and the distribution of its avian prey. *Landscape and Urban Planning* 127:94-103. doi:10.1016/j.landurbplan.2014.03.009.
3. **SUMASGUTNER, P.**, RUBIN, I., GAMAUF, A. (2014): Collecting blood samples in Eurasian Kestrels (*Falco tinnunculus*) (Aves: Falconidae) via blood-sucking bugs (Insecta: Hemiptera: Reduviidae) and their use in genetics and leucocyte profiles. *Ann. Naturhist. Mus. Wien, B* 116: 247-257.
4. **SUMASGUTNER, P.**, VASKO, V., VARJONEN, R., KORPIMÄKI, E. (submitted): Public information revealed by prey remains in nest-sites is more important than ectoparasite avoidance in the settlement decisions of Eurasian kestrels (*Falco tinnunculus*). *Behavioral Ecology and Sociobiology*.
5. MITTER, G., **SUMASGUTNER, P.**, GAMAUF, A. (submitted): Niche-partitioning in three *Apodemus* species in an urban environment. *Ann. Naturhist. Mus. Wien*.
6. **SUMASGUTNER, P.**, ZUNA-KRATKY T., KRENN H.W. (2010): Einfluss der Waldstruktur auf die Nistplatzwahl von Greifvögeln in den March-Auen/Niederösterreich. *Vogelwarte* 48: 81-95.

Book chapter:

7. **SUMASGUTNER, P.**, THOBY, A. (2011): Das Greifvogel- und Schwarzstorchvorkommen der March-Auen - Bestandsveränderungen, Habitatwahl und Schutzstrategien.[Birds of prey and the Black Stork in the Morava floodplains – population dynamics and habitat structure]. In: Steiner E, Dietrich C (eds) *Zu neuen Ufern: Hydrodynamik und Biodiversität in den March-Thaya-Auen*. Amt der Niederösterreichischen Landesregierung, Abt. Kultur und Wissenschaft, St. Pölten, Band 22: 99-128.

Published conference papers:

8. **SUMASGUTNER, P.**, KRENN, H.W., 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.
9. MITTER, G., **SUMASGUTNER, P.**, GAMAUF, A. (2013): City centre or periphery? Distribution and morphological adaptation of *Apodemus* taxa along an urban gradient. *Beiträge zur Jagd- und Wildforschung* 38: 305-319.
10. **SUMASGUTNER, P.**, KRENN, H.W., GAMAUF, A. (2011): Urbane Jäger im Aufwind? Habitatnutzung, Brutbiologie und Nahrungsökologie des Turmfalken (*Falco tinnunculus*) in Wien. *Vogelwarte* 49: 309-310.
11. **SUMASGUTNER, P.**, ZUNA-KRATKY, T., KRENN, H.W. (2009): Einflüsse der Waldstruktur auf die Habitatwahl von Greifvögeln in den Marchauen/Niederösterreich. *Vogelwarte* 47: 353 – 354.

In preparation:

SUMASGUTNER, P., GAMAUF, A., KRUCKENHAUSER, L. (in prep.): Sex in the City: Extra-pair paternity and genetic variability in Eurasian kestrels (*Falco tinnunculus*) in Vienna, Austria.