Beiträge zur
JAGD
&WILD
forschung · 38

Petra Sumasgutner, Harald W. Krenn, Vienna; Judith Düesberg, Berlin;
Tomislav Gaspar, Anita Gamauf, Vienna

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 characterized 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 specialized bird-feeders like the goshawk (*Accipiter gentilis*), the sparrowhawk (*Accipiter nisus*) or falcon species respond well to urban landscapes because of the large biomass 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 utilization 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 characterization 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 carotenoïd 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 hypothesize that urban Kestrels specialize 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 km^2 (Wichmann et al. 2009) the most abundant raptor in Vienna, Austria (415 km^2, 1.7 million inhabitants). This density is higher than in other European cities, e.g. 22.9–33.3 bp/100 km^2 in Berlin, Germany (Kupko et al. 2000) or 40–55 bp/100 km^2 in Paris, France (Malher et al. 2010), and higher than in rural areas in Austria with 8–30 bp/100 km^2 (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 per food, 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 orthophoto (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 organized nest-box program in Vienna; hence kestrels rarely use nest-boxes (5.6 %). Between 2010 and 2011 occup-

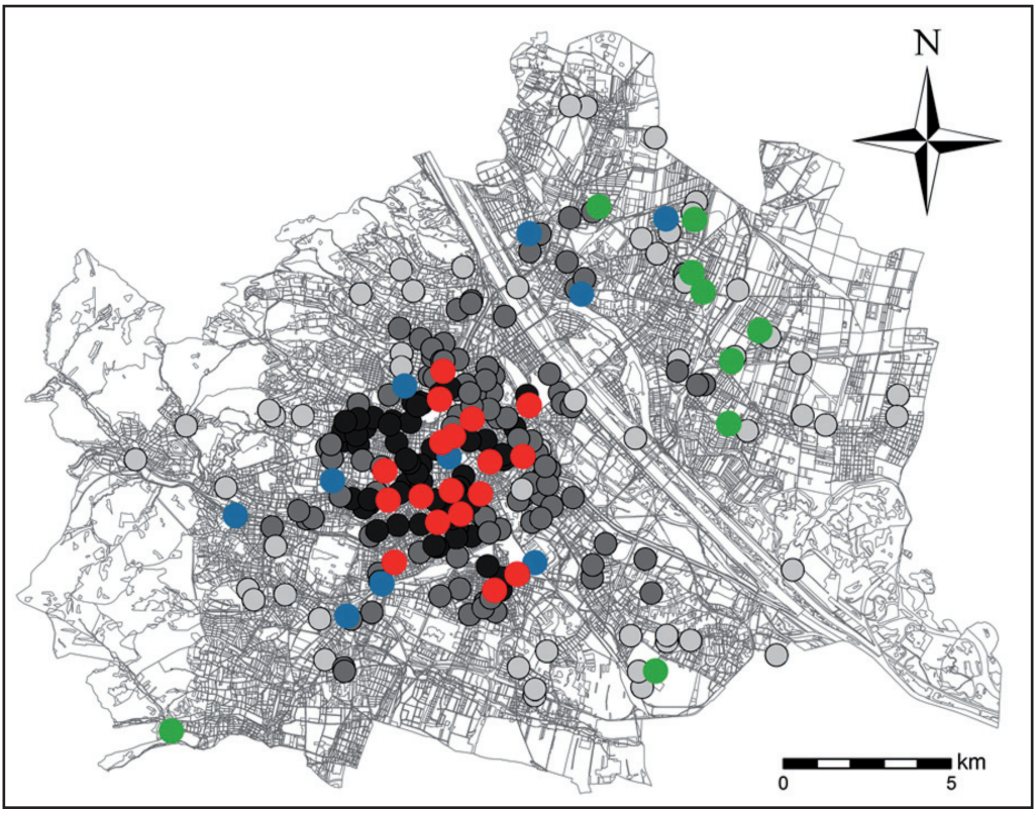

Fig. 1 Urban gradient and nest-sites of Falco tinnunculus in Vienna in 2010 (n = 251) according to percentage of sealed soil: city centre (black, 81–100 % soil sealing, n = 81), mixed zone (dark grey, 51–80 % soil sealing, n = 109) and suburban area (light grey, 1–50 % soil sealing, n = 61); white – 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 analyzed 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 $H = -\Sigma p_i \log p_i$, 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 $B = 1/\Sigma p_i^2$, where p_i is the proportion of the diet contributed by prey type i. Levin's index tends to weight in favor 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 urbanized 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 and 4 % insects and 4.2 % 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 analyzed. 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 pellet 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 analyzed (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 caerules, 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.

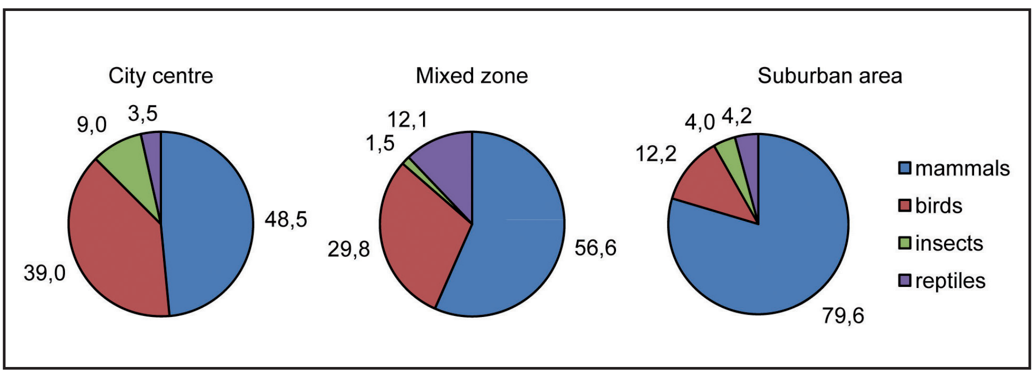

Fig. 2 Proportions of main prey categories in percent (based on calculated biomass of prey items) of kestrel pellets from three urban zones in Vienna: city centre (n = 18 nest-sites), mixed zone (n = 10 nest-sites) and suburban area (n = 9 nest-sites).

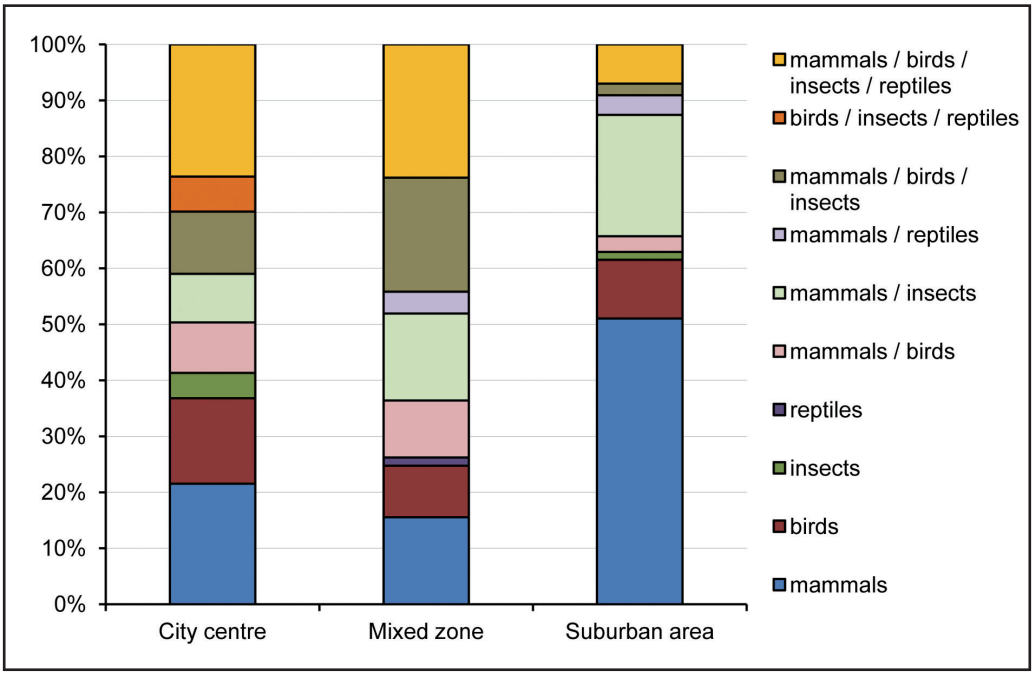

Fig. 3 Composition of kestrel pellets from three urban zones in Vienna (n = 637 pellets).

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.

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

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			
			City centre	Mixed zone	Suburban area	Total
Coleoptera	Buprestidae	Indet.	1	-	-	1
	Carabidae	*Calosoma* sp.	-	4	1	5
		Carabus sp.	20	6	-	26
		indet.	10	15	3	28
	Cerambycidae	indet.	-	2	3	5
	Coccinellidae	indet.	1	1	-	2
	Curculionidae	*Phyllobius* sp.	1	-	-	1
		indet.	8	5	2	15
	Dytiscidae	indet.	1	2	-	3
	Elateridae	indet.	2	-	1	3
	Geotrupidae	*Geotrupes* sp.	2	-	-	2
		indet.	2	7	-	9
	Histeridae	indet.	10	-	-	10
	Lucanidae	indet.	1	1	2	4
	Scarabaeidae	*Cetonia aurata*	35	33	10	78
		Oxythyrea sp.	-	1	-	1
		Potosia sp.	-	2	-	2
		Melolontha sp.	1	-	-	1
		indet.	8	-	1	9
	Silphidae	indet.	1	1	-	2
	Staphylinidae	indet.	1	-	-	1
	indet.		48	57	11	116
Orthoptera	Gryllidae	*Gryllus campestris*	-	-	1	1
	Gryllotalpidae	*Gryllotalpa gryllotalpa*	-	2	3	5
	Phaneropterinae	indet.	-	2	-	2
	Tettigoniidae	indet.	15	5	-	20
	indet.		4	2	6	12
Hymenoptera	Apidae		-	1	-	1
	Crabronidae	*Philanthus* 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 ± 6.3 days	May 3 ± 11.9 days	Mai 1 ± 17.6 days	0.13	0.9387
clutch size	2.52 ± 2.06	4.58 ± 1.73	5.00 ± 1.41	8.53	**0.0140**
hatched	1.74 ± 1.94	3.58 ± 1.78	4.40 ± 1.14	10.00	**0.0067**
fledged	1.00 ± 1.33	1.58 ± 1.31	4.00 ± 1.22	11.14	**0.0038**
2011 (*n* = 52)					
laying date	May 4 ± 14.4 days	May 3 ± 15.1 days	April 19 ± 7.2 days	6.18	**0.0454**
clutch size	3.88 ± 1.86	4.46 ± 1.48	5.75 ± 1.16	7.70	**0.0213**
hatched	2.38 ± 2.42	3.57 ± 1.89	4.25 ± 2.71	4.82	0.0900
fledged	1.81 ± 1.94	2.61 ± 1.79	3.50 ± 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 specialized 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 characterized 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 leaded 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 cached 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 favor 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 need further investigations of diet specialization 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 present 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 carotenoïd 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). Carotenoïds serve important health-related physiological functions (Chew and Park 2004), but see also Costantini and Møller (2008). As vertebrates cannot synthesize 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 coloration 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 carotenoïd concentration, whereas birds and mainly insects are carotenoïd rich (Goodwin 1980). In urban kestrels, carotenoïd poor resources (voles, mice and shrews) are potentially traded for carotenoïd 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 carotenoïd source in nestlings' diet.

Acknowledgements

The study was performed under license from the Ethics-Committee of the University of Veterinary Medicine and the Environmental Protection Bureau of Vienna (MA 22/1263/2010/3) which also provided the land utilization map (MA22/709/2010). The project was funded by the Austrian Academy of Science (DOC-fFORTE grant), the University of Vienna (Doctoral Research Fellowship) and the Vienna Science and Technology Fund. We thank the following contributors for helping with the determination of prey species and information to the distribution of potential prey species in Vienna: Simon Engelberger, Julia Gstir, Anna Nele Herdina, Gerda Mitter, Katharina Spreitzer and Thomas Zuna-Kratky.

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 confirms. 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 specialized 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. Analyzing 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 der Turmfalken (*Falco tinnunculus*) wurde entlang eines Urbangradienten in der Großstadt Wien, Österreich untersucht. Die Studie basiert auf Gewöllen und Rupfungen, die während der Brutsaisonen 2010–2011 gesammelten 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 Kleinsäugern 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 Kleinsäugern 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 Ausflugraten mit zunehmender Beutediversität von der Peripherie in Richtung Stadtzentrum.

References

Arroyo, B.E. (1997): Diet of Montagu's Harrier *Circus pygargus* in central Spain: analysis of temporal and geographic variation. – Ibis **139**: 664–672.

Berry, M.E.; Bock, C.E.; Haire, S.L. (1998): Abundance of Diurnal Raptors on Open Space Grasslands in an Urbanized Landscape. – The Condor **100**: 601–608.

Blotzheim, G. v. and Bauer, K.M. (1980): Handbuch der Vögel Mitteleuropas. Columbiformes – Piciformes. – Aula-Verlag, Wiesbaden.

Boratynski, Z.; Kasprzyk, K. (2005): Does urban structure explain shifts in the food niche of the Eurasian Kestrel (*Falco tinnunculus*)? Buteo **14**: 11–17.

Bortolotti, G.R.; Tella, J.L.; Forero, M.G.; Dawson, R.D. and Negro, J.J. (2000): Genetics, local environment and health as factors influencing plasma carotenoids in wild American kestrels (*Falco sparverius*). – Proceedings of the Royal Society of London. Series B: Biological Sciences **267**: 1433–1438.

Cade, T.J.; Martell, M.; Redig, P.; Septon, G. and Tordoff, H. (1996): Peregrine Falcons in urban North America. – In: Bird, D.M.; Varland, D.E. and Negro, J.J. (eds.) p. 3–13. – Raptors in human landscapes: adaptations to built and cultivated environments. Adaptations to built and cultivated environments. – Academic Press, London.

Casagrande, S.; Costantini, D.; Fanfani, A.; Tagliavini, J. and Dell'Omo, G. (2007): Patterns of serum carotenoid accumulation and skin colour variation in kestrel nestlings in relation to breeding conditions and different terms of carotenoid supplementation. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology **177**: 237–245.

Casagrande, S.; Csermely, D.; Pini, E.; Bertacche, V. and Tagliavini, J. (2006): Skin carotenoid concentration correlates with male hunting skill and territory quality in the kestrel *Falco tinnunculus*. – Journal of Avian Biology **37**: 190–196.

Chace, J.F. and Walsh, J.J. (2006): Urban effects on native avifauna: a review. – Landscape and Urban Planning **74**: 46–69.

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

Chew, B.P. and Park, J.S. (2004): Carotenoid Action on the Immune Response. – The Journal of nutrition **134**: 257S–261S.

Costantini, D. and Møller, A.P. (2008): Carotenoids are minor antioxidants for birds. – Functional Ecology **22**: 367–370.

Düesberg, J. (2012): Video analysis versus prey analysis – method comparison to study feeding ecology of urban Kestrels *Falco tinnunculus* [German with English summary]. – Bachelor thesis. Humboldt Universität zu Berlin, Berlin.

Eck, S.; Fiebig, J.; Fiedler, W.; Heynen, I.; Nicolai, B.; Töpfer, T.; van den Elzen, R.; Winkler, R. and F. Woog, F. (2011): DO-G Deutsche Ornithologen-Gesellschaft: Measuring Birds – Vögel vermessen. – Chist Media Natur.

Galanos, I. (1991): Beitrag zur Lebensweise des Turmfalken (*Falco tinnunculus*) in urbanen Ökosystemen und zur Kenntnis anthropogener Einflüsse auf die Population am Beispiel der Stadt Frankfurt am Main. – Dissertation. Universität Frankfurt/Main, Frankfurt/Main.

Gamauf, A. (1991): Greifvögel in Österreich. Bestand – Bedrohung – Gesetz. – Umweltbundesamt Wien, Wien.

Goodwin, T.W. (1980): The Biochemistry of the Carotenoids. 2nd edition. – Chapman and Hall, London; New York.

Kenward, R. (2006): The Goshawk. – T & A D Poyser, London.

Kirkwood, J.K. (1991): Energy requirements for maintenance and growth of wild mammals, birds and reptiles in captivity. – The Journal of nutrition **121**: 29–34.

Kjellander, P. and Nordström, J. (2003): Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. – Oikos **101**: 338–344.

Korpimäki, E. (1985): Diet of the Kestrel *Falco tinnunculus* in the breeding season. – Ornis Fennica **62**: 130–137.

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

Kostrzewa, R. and Kostrzewa, A. (1993): Der Turmfalke. Überlebensstrategien eines Greifvogels. – Aula Verlag, Wiesbaden.

Krebs, C.J. (2004): Ecological methodology. 2 edition. Benjamin / Cummings, Menlo Park, California.

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

Kupko, S.; Schlottke, L. and Rinder, J. (2000): Der Turmfalke (*Falco tinnunculus* L.) im Berliner Stadtgebiet – Eine Auswertung unter besonderer Berücksichtigung der Monitoringfläche Nr. 376 (Berlin-West). – Populationsökologie Greifvogel- und Eulenarten **4**: 359–372.

Lack, D. (1954): The Natural Regulation of Animal Numbers. – Clarendon Press, Oxford.

Levins, R. (1968): Evolution in changing environments; some theoretical explorations. – Princeton University Press, Princeton, N.J.

Mägi, M.; Mänd, R.; Tamm, H.; Sisask, E.; Kilgas, P. and Tilgar, V. (2009): Low Reproductive Success of Great Tits in the Preferred Habitat: A Role of Food Availability. – Ecoscience **16**: 145–157.

Malher, F.; Lesaffre, G.; Zucca, M. and Coatmeur, J. (2010): Oiseaux nicheurs de Paris. Un atlas urbain. – Corif. Delachaux et Niestlé, Paris.

Mebs, T. and Schmidt, D. (2006): Die Greifvögel Europas, Nordafrikas und Vorderasiens. – Franckh-Kosmos Verlag, Stuttgart.

Mitter, G. (2012): Kleinsäuger im Wiener Stadtgebiet: Der Einfluss öffentlicher Parks und Grünanlagen auf Häufigkeit und Morphologie [German with English summary]. – Master thesis. Universität Wien, Wien.

Newton, I. (1980): The role of food in limiting bird numbers. – Ardea **68**: 11–30.

Olson, V.A. and Owens, I.P.F. (1998): Costly sexual signals: are carotenoids rare, risky or required? Trends in Ecology & Evolution **13**: 510–514.

Piattella, A.; Salvati, L.; Manganaro, A. and Fattorini, S. (1999): Spatial and temporal variations in the diet of the Common Kestrel (*Falco tinnunculus*) in Rome, Italy. – Journal of Raptor Research **33**: 172–175.

Riegert, J. and Fuchs, R. (2004): Insects in the diet of urban kestrels from central Europe: An alternative prey or constant component of the diet? – Ornis Fennica **81**: 23–32.

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

Riegert, J.; Lövy, M. and Fainová, D. (2009): Diet composition of Common Kestrels *Falco tinnunculus* and Long-eared Owls *Asio otus* coexisting in an urban environment. – Ornis Fennica **86**: 123–130.

Sachslehner, L.M. (1996): „Nachtaktiver" Turmfalke (*Falco tinnunculus* L.) jagt Eulenfalter am beleuchteten Stephansdom in Wien. – Können Turmfalken im oberen UV-Bereich sehen? – Ökologie der Vögel **18**: 55–64.

Salvati, L.; Manganaro, A.; Fattorini, S. and Piattella, E. (1999): Population features of kestrels *Falco tinnunculus* in urban, suburban and rural areas in central Italy. – Acta Ornitholigica **34**: 53–58.

Shrubb, M. (1993): Nest Sites in the Kestrel *Falco tinnunculus*. – Bird Study **40**: 63–73.

Sieber, J. and Uibel, G. (1998): Die geschützten Säugetiere Wiens (ausgenommen Fledermäuse) – Artenportraits. Page 45. – Magistratsabteilung 22, Wien.

Smith, R.M.; Thompson, K.; Hodgson, J.G.; Warren, P.H. and Gaston, K.J. (2006): Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. – Biological Conservation **129**: 312–322.

Stephen, D.W. and Krebs, J.R. (1986): Foraging theory. Monographs in behavior ecology. – Princeton University.

Sternalski, A.; Mougeot, F.; Eraud, C.; Gangloff, B.; Villers, A. and Bretagnolle, V. (2010): Carotenoids in nestling Montagu's harriers: variations according to age, sex, body condition and evidence for diet-related limitations. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology **180**: 33–43.

Tella, J.L.; Hiraldo, F.; Donazar-Sancho, J.A. and Negro, J.J. (1996): Costs and benefits of urban nesting in the lesser kestrel. – In: Bird, D.M.; Varlan, D.E. and Negro, J.J. (eds). Raptors in Human Landscapes, Adaptations to Built and Cultivated Environments. – Academic Press, New York p. 53–60.

Village, A. (1990): The Kestrel. – T & A D Poyser, London.

Wichmann, G.; Dvorak, M.; Teufelbauer, N. and Berg, H.-M. (2009): Die Vogelwelt Wiens – Atlas der Brutvögel. –Verlag Naturhistorisches Museum Wien, Wien.

Witt, K. (2000): Situation der Vögel im städtischen Berlin. – Vogelwelt **121**: 107–128.

Addresses of authors:

Petra Sumasgutner*
Tomislav Gaspar
Anita Gamauf
Department of Integrative Zoology
University of Vienna
Althanstraße 14, 1090 Vienna, Austria
und
Museum of Natural History Vienna
1st Zoological Department
Burgring 7, 1010 Vienna, Austria

Harald W. Krenn
Department of Integrative Zoology
University of Vienna
Althanstraße 14, 1090 Vienna, Austria

Judith Düesberg
Humboldt-University of Berlin
Invalidenstraße 43, 10115 Berlin, Germany

* corresponding author

E-Mail: petra.sumasgutner@univie.ac.at