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3 authors:


Peter Mikula
Technical University of Munich


Martin Hromada
University of Presov in Presov


Piotr Tryjanowski
Poznań University of Life Sciences

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Bats and Swifts as food of the European Kestrel (*Falco tinnunculus*) in a small town in Slovakia

Peter Mikula*, Martin Hromada & Piotr Tryjanowski

*P. Mikula, Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 43 Praha 2, Czech Republic. *Corresponding author's e-mail: petomikula158@gmail.com*
M. Hromada, Department of Ecology, Faculty of Humanities and Natural Sciences, University of Prešov, 17th November 1, 081 16 Prešov, Slovakia, and Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71 C, 60-625 Poznań, Poland
P. Tryjanowski, Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71 C, 60-625 Poznań, Poland

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Bats (Chiroptera) and Common Swifts (*Apus apus*) are excellent fliers that use buildings as roosts and breeding sites in urban areas. Some predators have recently become adapted to hunting formerly unavailable prey. One such urban predator is the European Kestrel (*Falco tinnunculus*). We analyzed the diet and foraging behaviour of this species in Bardejov, North-Eastern Slovakia. In several observed breeding pairs, some bird began to hunt bats using novel foraging behaviour: sit-and-wait above ventilation channels of building facades where bats roosted, using ambush and perching tactics. Kestrel pairs that specialised in hunting bats also hunted Swifts. We did not find significant differences between Kestrel sexes in hunting bats and Swifts, but Kestrels preying on bats and Swifts had significantly higher breeding success than those that did not. Recently, Kestrels and their novel prey, bats and Swifts, have become endangered by rapidly-improved insulation of building facades in Central Europe. This intervention simultaneously destroys breeding and roosting places and potentially causes the collapse of urban populations of the European Kestrel.

1. Introduction

Urban environments offer animals new opportunities, including novel food resources and safe shelters. The main reasons for favouring cities over natural habitats are reduced predation risk (Tomiałojć 1980, 1982, Shochat 2004, Jokimäki *et al.* 2005, Kark *et al.* 2007) and reduced food stress (Partecke *et al.* 2006). Animals that have adapted to life in cities often utilise buildings as breeding and roosting sites; this strategy is common in birds and bats (Marzluff *et al.* 2008). New environments provide new possibilities, which can lead to the emergence of different prey choices or behavioural adaptations, such as novel foraging techniques. Opportunistic innovations reflect species behavioural plasticity and a tendency to use novel means to solve problems (Lefebvre *et al.* 1997).

One such behaviourally plastic urban pioneer is the European Kestrel (*Falco tinnunculus*). It is a small, opportunistic raptor with reversed sexual dimorphism and is widespread throughout the Palaearctic region (Village 1990, 1998). The feeding behaviour of this species is highly individualistic (Costantini *et al.* 2005). The species consumes a variety of prey, such as arthropods, lizards, birds and small mammals (Cruz 1976, Village 1990, Negro *et al.* 1992, 2000, GilDelgado *et al.* 1995, Romanowski 1996, Aparicio 2000, Żmihorski & Rejt 2007). The diet is dominated by voles, but also frequently includes insects (Yalden & Warburton 1979, Korpimäki 1985, Darolová 1989, Korpimäki & Norrdahl 1991, Riegert & Fuchs 2004, Riegert *et al.* 2007, Kečkéšová & Noga 2008).

Kestrels have occasionally been observed to hunt prey-species that are difficult to catch, such as bats and Swifts (Black 1976, Speakman 1991, Speelman *et al.* 1995, Tol 2001, Kečkéšová & Noga 2008). Here, we describe how Kestrels learned to catch bats in new ways and how these same birds subsequently became adapted to hunting prey with a similar mode of living, namely the Common Swift (*Apus apus*).

We hypothesized that Kestrels (pairs or individuals) that intensively hunt bats also more frequently catch Swifts. We also tested sexual differences in Kestrels related to the hunting and breeding success of pairs specialised in catching bats and Swifts. Finally, we evaluated the breeding success of bat/Swift-hunting pairs living in breeding territories in which buildings were undergoing insulation renovation to see if this intervention impacted the local population.

2. Material and methods

2.1. Study area

We conducted the research in Bardejov (49° 17'34" N, 21°16'40" E), a small town (33,000 inhabitants, 73 km^2) in North-Eastern Slovakia during breeding seasons 2005–2011. Bardejov is located at the transition zone between the Eastern and Western Carpathians, in a broad valley amongst mountain ranges of Nízke Beskydy, Ondavská vrchovina and Čergov. The lower parts of valleys are largely comprised of agricultural fields which, due to topographic conditions, are traditionally smaller than in the lowlands, with many wind shelterbelts and groups of bushes and trees. Forested areas are represented by bank growths along creeks and rivers, and continuous forests can be found on hilltops and mountain chains. Approximately 40% of the area surrounding the town is covered by forests.

We observed breeding pairs of Kestrels at 12 nesting sites. The studied birds live in the medieval, fortified town center (UNESCO World Heritage List) where they use a variety of buildings as breeding sites e.g., a church, bastions and historic buildings (five breeding localities), new apartment buildings (five breeding localities), an old factory complex (one locality), and a suburban village (one locality). Kestrels began to colonize Bardejov's urban habitats in the 1970s at the latest (collection of Sarisske Museum in Bardejov, see Hromada *et al.* 2003; two birds collected within town intravilane in 1976 and 1977). T. Weisz, curator of the museum, does not mention Kestrels breeding within town (Weisz 1967).

However, according the same author it seems that bats and Swifts colonized the town before Kestrels – they inhabited church towers and house lofts (Weisz 1967). In 1950s and 1960s in Czechoslovakia began the era of concrete-element buildings. Facades of these towering housings, common in Slovakia and elsewhere in the former Soviet bloc, have abundant ventilation openings and other crevices. Such facades provide abundant breeding sites and shelter for bats and Swifts. Similarly to other Slovak towns, the population of bats and Swifts in Bardejov has remained relatively stable until recently (Ceľuch & Kaňuch 2002).

2.2. Pellet collection and observations

We collected field observations of Kestrels during 2005–2011 in Bardejov and surrounding areas, using 8 × 30 binoculars. We conducted 2–3 observation periods per week (ca 650 observations, 3,500 hours in total) on the ground or on building roofs, during the morning (between one hour before and two hours after sunrise), during the day (between one hour before until one hour after midday) and during the evening (1–2 hours before until one hour after the sunset). We applied unfixed observation times due to changes in day length during the year. All three categories were represented equally in terms of observational hours.

All Kestrel pairs predominantly hunted voles, but for this study we focused on bat and Swift hunts. Individuals and pairs hunted bats or Swifts using three major techniques: (1) flight hunting (Kestrel flies around buildings and attacks bats/Swifts when they fly out from the shelter); (2) sit-and-wait hunting (Kestrel sits on top of a building, about 0.5 m above a ventilation opening where bats/Swifts roost; as bats/Swifts fly out, the Kestrel attempts to catch them; bats and Swifts are unable to see the ambushing Kestrel; this technique was not used for hunting other prey); and (3) ventilation-opening perching (Kestrel perches at a ventilation opening and waits for bats/Swifts to leave their roost; sometimes we observed Kestrels sticking one of their legs into the opening in an attempt to pull out the prey).

We recorded predation on bats and Swifts in Kestrel territories with high densities of these prey. Hunts at dusk were observed in the light of street lamps. We recorded a total of 163 observations of Kestrels hunting bats (128 observations) and Swifts (35 observations). We also recorded the Kestrels' sex, hunting technique, success and prominent behaviour, such as neophobia. Neophobic behaviour refers to situations in which an individual Kestrel displays explicit uncertainty or surprise to novel prey. Such behaviour included a Kestrel shuffling on its feet, or switching a captured prey item repeatedly between bill and foot. We also recorded the number of fledglings for each Kestrel pair in order to evaluate their breeding success. We were not able to identify individual birds because they had not been marked.

We collected pellets once a month in June, July and August at three nesting sites in 2009 and seven sites in 2010. Pairs nested relatively close to each other and their hunting territories often overlapped. For that reason we collected pellets under nests only: we cleared each site one month prior to pellet collection which enabled us to include only fresh pellets into the analysis. We determined prey items according to Anděra & Horáček (2005) using an STM 701 stereo-microscope. We divided prey items into eight categories: bats (Chiroptera), beetles (Coleoptera), Common Swifts (*Apus apus*), grasshoppers (Orthoptera), insects (Insecta), reptiles (Reptilia), small passerines (Passeriformes) and small rodents (Micromammalia).

We also tested the breeding success of Kestrels in relation to their ability to catch bats and Swifts, and in relation to facade insulation of apartment buildings, which is known to have decimated bat and Swift populations in the city (Celuch 2012, Vávrová 2012). Insulation operations of some studied buildings were conducted gradually in 2008, 2009 and 2010. In most cases, thermal insulation took place during the same season and covered extensive parts (up to 60% in one season) of buildings in the breeding territories of the studied Kestrels. However, we did not know whether the breeding success of Kestrels would be affected by these operations *per se* or be a consequence of declining numbers of bats and Swifts (or both). Therefore, we analyzed periods prior to, during, and after insulation. Due to the small sample size, we combined data into one model for the whole study period. We considered the number of fledglings as an ordinal discrete variable and therefore applied mostly non-parametric tests (Mann-Whitney to pair comparison between Kestrel pairs hunting and not hunting bats and/or Swifts; Friedman ANOVA to compare number of fledglings in the same nest locations before, during and after buildings insulation; Kendall tau correlation). In one case we did a permutation based sign-test (Manly 1997). All statistical tests were two-tailed, and were run using the SPSS 17.0 package.

3. Results

First cases of Kestrel hunting for prey dwelling in ventilation openings (bats and Swifts) on building facades in Bardejov were observed in 2006. In May, we first observed one male to attack a bat, but from June onwards a female joined its partner, and soon both hunted bats (*Nyctalus noctula, Plecotus* sp.) in flight around buildings. In the next season (late in July), we observed the male to hunt Swifts by sit-and-wait technique, perched on ventilation-opening shelf. This series of observations involved only one pair, but similar behaviour was observed at other breeding localities in subsequent years, with a maximum of eight pairs hunting bats in 2008.

Attacks by Kestrels on bats (128 in total) occurred mainly at or after dusk (89 cases, 69.5%); 32 (25.0%) occurred in the early morning and seven (5.5%) during daytime hours. We also re-

Table 1. The European Kestrel's (*Falco tinnunculus*) diet in Bardejov, Slovakia.

Taxon	No. prey items	% in pellets
Insecta[1]	23	5.2
Coleoptera[2]	41	13.4
Orthoptera[3]	113	15.0
Reptilia[4]	2	0.5
Passeriformes[5]	14	3.3
Apus apus	25	5.6
Chiroptera[6]	16	3.8
Micromammalia[7]	406	85.2
Prey items, total	640	
Pellets, total	426	

1) Ephemeroptera, Hymenoptera; 2) *Melolontha melolontha*, *Selatosomus* sp., beetles; 3) Ensifera, *Decticus* sp., Acrididae; 4) *Zootoca vivipara*; 5) *Parus major*, *Passer domesticus*, *Phoenicurus ochruros*, *Turdus merula*; 6) *Nyctalus noctula*, *Plecotus* sp.; 7) *Microtus* sp., *Mus musculus*, *Myodes glareolus*, *Sorex minutus*

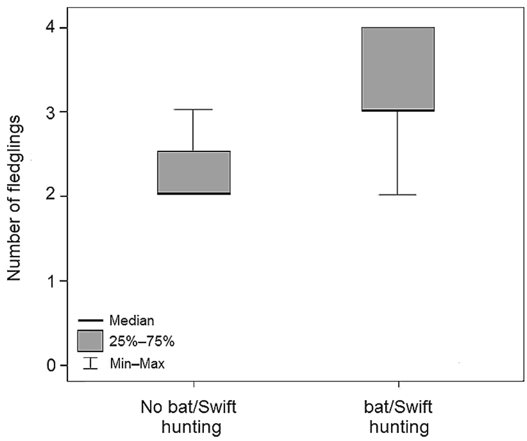

Fig. 1. Breeding success in the European Kestrel pairs that hunted vs. did not hunt bats and Common Swifts in Bardejov, Slovakia during 2005–2011.

corded 35 direct observations of Kestrels hunting Swifts. 31 (88.6%) attacks occurred during daytime hours and four (11.4%) occurred in the morning ($\chi^2 = 19.31$ with Yates correction, $df = 1$, $p < 0.001$).

3.1. Hunting technique

In 36 cases (28.1% of all observations) Kestrels hunted bats in flight. Additionally, Kestrels used the sit-and-wait strategy to catch bats in 63 cases (49.2%), and 29 cases (22.7%) concerned perching at the entrance of ventilation openings. Swifts were taken using several different strategies: by the sit-and-wait technique (21 cases; 60.0%) and by perching at ventilation openings (14 cases; 40.0%). We never observed Kestrels attacking Swifts in flight.

3.2. Food analysis

We collected 426 pellets and identified 640 prey items at Kestrel nests. The most frequent prey were small mammals, followed by grasshoppers, beetles, other insects, Common Swifts, bats, passerines and lizards (Table 1). We also collected prey remnants under nests: five individuals of small passerines, 12 bats and six voles (*Microtus* sp.).

In eight out of twelve breeding sites, Kestrels hunted bats and/or Swifts. All bat- and/or Swift-hunting Kestrel pairs first started to hunt bats and subsequently included Swifts in their diet. There were no significant differences between male and female Kestrels in bat- and/or Swift-hunting success ($\chi^2 = 0.10$ with Yates correction; $df = 1$, $p = 0.75$, $n = 163$, only bat- and/or Swift-hunting pairs included). Kestrels specialised in bat hunting also specialised in catching Swifts (Kendall tau correlation, $\tau = 0.66$, $p < 0.05$, $n = 10$). However, we did not find significant correlations with other prey types ($p > 0.3$ in all cases).

Kestrel pairs that specialised in bat and/or Swift hunting had higher breeding success than those that did not hunt bats and Swifts (Mann-Whitney *U* test, $Z = -5.134$, $p < 0.0001$; $n = 21$ and 44, mean ± SD = 3.29 ± 0.56 and 2.05 ± 0.75, respectively; Fig. 1). Pairs that hunted bats or Swifts occurred only at localities with high density of this type of prey (i.e., mainly in the historic town centre and urban areas with a high proportion of towering buildings).

The breeding success of Kestrel pairs hunting for bats and/or Swifts decreased significantly after insulation of buildings (Friedman's ANOVA, $F_{2,5} = 8.444$, $p = 0.015$; mean breeding successes ± SD before, during and after insulation 3.4 ± 0.55, 3.6 ± 0.55 and 2.0 ± 0.0, respectively; Fig. 2). In this analysis we included five pairs, of which two had been subjected to insulation within their territory

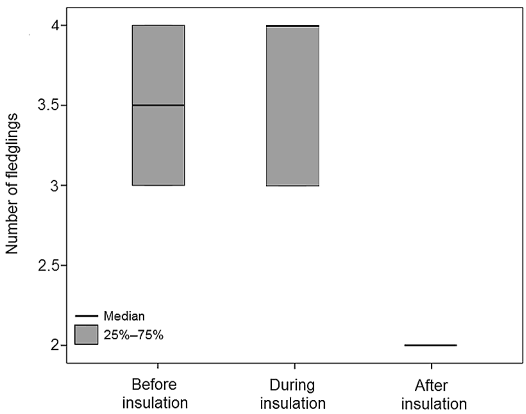

Fig. 2. Breeding success in the European Kestrel pairs hunting for bats and Common Swifts year before, during and after facade insulation of buildings occupied by Kestrels, bats and Common Swifts in Bardejov, Slovakia. In some cases, insulation continued over several years. For two Kestrel pairs, insulation began in 2008, for one in 2009, and for another two in 2010.

in 2008, one in 2009 and two in 2010. Two additional Kestrel pairs stopped breeding following insulation. Hence, the effect of insulation (and not year-to-year variation) seems likely to have negatively impacted breeding success.

Kestrels occasionally displayed neophobic behaviour when they hunted a bat or Swift. This behaviour was significantly more likely during the first observed encounters with novel prey comparing to subsequent encounters (sign test, $p = 0.008$; 10,000 Monte Carlo permutations, $p = 0.004$, $n = 16$).

4. Discussion

Urban areas offer new possibilities for species which are able to cope with changing environments. Occupying new man-made niches demands behavioural flexibility. Bats and Swifts have adopted ventilation openings on building facades as roosting sites (Bihari 2004, Ceľuch *et al.* 2006). We found that some individuals of the European Kestrel were able to adjust their hunting techniques to local conditions in order to maximize their breeding success, and learned to effectively catch both bats and Common Swifts.

In general, bats, due to their nocturnal activity and agile flight, are rather rarely preyed upon by predators (Speakman *et al.* 2000). Indeed, Jędrzejewska & Jędrzejewski (1998) have characterized bats as UFO – "uncatchable flying objects" for birds. The few bat-hunting predators with nocturnal activity include owls (Caire & Ports 1981). Diurnal raptors, such as the Bald Eagle (*Haliaeetus leucocephalus*), Lesser Kestrel (*Falco naumanni*) and Peregrine Falcon (*Falco peregrinus*), have often been recorded to forage at night (Kaiser 1989, Negro *et al.* 2000, DeCandido & Allen 2006). Tryjanowski & Lorek (1998) have observed that the European Kestrel, at least occasionally, also hunts at and after dusk. In Bardejov Kestrels have been observed to hunt only from the sunset until one hour after dark, with no hunting attempts observed after this period. During daytime hours, bats are predated rarely and only by a few species, such as the European Hobby (*Falco subbuteo*), Peregrine Falcon (*Falco peregrinus*) and White-breasted Hawk (*Accipiter chionogaster*) (Baker 1962, Byre 1990, Dronneau & Wassmer 2005, Dronneau & Wassmer 2008, Stevens *et al.* 2009, Jenner 2010). However, all of those observations were at sites with large concentrations of bats. Indeed, bats are rarely vulnerable to predation, exceptions to this are when they are roosting or travelling in dense aggregations (Caire & Ports 1981, Rodriguez-Duran & Lewis1985).

We found that Kestrels in Bardejov hunted bats not only in the air or using a sit-and-wait strategy, as reported by Yosef (1991), Negro *et al.* (1992), Dronneau & Wassmer (2005, 2008) and Rodriguez-Duran & Lewis (1985) for other falconids, but also using ambush hunts from above ventilation openings, and perching at these openings. We suggest that these behaviours are true foraging innovations and demonstrate ecological plasticity in the European Kestrel (Morse 1980). The propagation of such innovations throughout the population still remains poorly understood. Ecologically innovative behaviour can involve both the selection of new food resources as well as the employment of specialised behaviour (Greenberg 2003). Such innovations can help organisms to cope with changes in the environment (Reader & Laland 2003, Boogert *et al.* 2008). Although our data appear largely anecdotal, they demonstrate the spread of innovations throughout a local population (Fisher & Hinde 1949, Lefebvre 1995). The documented behavioural change, such as the ability to catch prey by novel hunting techniques, also positively influenced the breeding success of such innovative pairs.

Flight-hunting is a dominant foraging technique in the European Kestrel (Rijnsdorp *et al.* 1981). However, Rudolph (1982) and Pettifor (1983) have shown that perch-hunting is less costly than hunting during hovering. Therefore, we suggest that the behavioural modifications reported here also represent optimization of foraging efficiency.

Kestrels that hunted bats also hunted Swifts, and they also found it easier to catch bats than Swifts. This may be because Swifts leave the roost more rapidly (Oehme 1968, Norberg 1976, Shiel *et al.* 1999). We propose that the ability to hunt bats prepares the Kestrels for catching Swifts.

During this study a substantial proportion of buildings with nests were renovated and their facades were covered with thermal insulation. Extensive insulation of buildings is rapidly becoming widespread in central European towns and strongly affects the dynamics of bat and Swift hunting in local Kestrel populations. Insulation causes decimation of bat and Swift populations (Ceľuch 2012, Vávrová 2012) which has consequences for the diet niche breadth of European Kestrels.

Urban environments offers new types of shelter for bats and Swifts, but predators also attempt to maintain their positions in this arms race. New man-made niches may appear quickly, but they can also disappear rapidly with significant effects on fauna adapted to these conditions, as our study has demonstrated. In the recent past, Kestrels, bats and Swifts inhabited churches. However, these places are also being renovated and entrances for birds and bats are closed off, forcing them to shift to modern buildings.

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Lepakot ja tervapääskyt tuulihaukan (*Falco tinnunculus*) saaliina pienessä Slovakialaisessa kaupungissa

Lepakot (Chiroptera) ja tervapääskyt (*Apus apus*) ovat varsin taitavia lentäjiä, jotka käyttävät urbaanien alueiden rakennuksia lepo- ja pesimäpaikkoina. Tuulihaukka (*Falco tinnunculus*) on yksi niistä urbaaneista pedoista, jotka ovat viime aikoina sopeutuneet saalistamaan aiemmin tavoittamattomissa olleita lajeja.

Analysoimme tuulihaukan ruokavalioa ja saalistuskäyttäytymistä Bardejovissa, koillisessa Slovakiassa. Monilla pareilla havaittiin, että ainakin toinen linnuista ryhtyi saalistamaan lepakoita uudella menetelmällä, käyttäen väijytysmäistä taktiikkaa, jossa istutaan rakennusten fasaadien venttiilikäytävien yläpuolella odottamassa niissä pesivien lepakoiden ilmestymistä. Tuulihaukkaparit jotka saalistivat lepakoita saalistivat myös tervapääskyjä.

Emme löytäneet merkitsevää sukupuolten välistä eroa lepakkojen ja tervapääskyjen saalistuksessa, mutta niillä tuulihaukoilla jotka saalistivat lepakoita ja tervapääskyjä oli muihin verrattuna parempi pesimämenestys. Viime aikoina nopeasti lisääntynyt fasaadien eristäminen uhkaa tuulihaukkaa ja sen uusia saalislajeja. Tämä tuhoaa samanaikaisesti sekä lepo- että pesimäpaikkoja uusilta saalislajeilta ja saattaa aiheuttaa urbaanien tuulihaukkapopulaatioiden romahduksen.

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