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How urban Kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation?

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Abstract. The hunting ranges of 34 male urban Kestrels were studied in a small city (40 km²) in S Bohemia (Czech Republic). It was assumed that males from the city center and periphery hunt for voles mainly on the city's outskirts. The "city-center" males are unable to defend their hunting ranges on the periphery because of aggression on the part of the "periphery" Kestrels. To counter this, they may either 1) invade the hunting ranges of periphery males or 2) establish their own exclusive hunting ranges. Our data supported the first suggestion. Hunting range size varied greatly, from 0.8 to 25.0 km² (7.2 ± 6.9 km²), with large overlaps of between 0.3% and 51.4% ($12.5 \pm 11.6\%$). The ranges of city-center males were several times larger than those of the periphery males, and greatly overlapped the ranges of other city center and periphery males. Overlapping of the hunting ranges of periphery males was less extensive. The higher energy costs in terms of flying to distant suitable hunting areas and frequent changes of hunting grounds should decrease the preference for nesting in the city center. Therefore, we suggest that Kestrels derive other advantages from living in the city center (e.g., the high quality of nest sites). Cohabitation, whereby city center males invade the hunting grounds of periphery males, appears to be a more effective strategy than partitioning.

Key words: Kestrel, *Falco tinnunculus*, urban, hunting range

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INTRODUCTION

Among European raptors, the Common Kestrel colonized cities most successfully (Cramp & Simmons 1980). Their breeding densities in cities are higher than farmland populations (Plesník 1992, Salvati et al. 1999). Studies of urban Kestrels in large European cities usually indicate a high proportion of birds in the diet (Yalden 1980, Darolová 1986, Quere 1990, Plesník 1992, Romanowski 1996, Kübler et al. 2005). On the other hand, voles still comprise a considerable part of Kestrel diet in these cities (i.e. Plesník 1992, Romanowski 1996, Rejt et al. 2000). Voles are not available in the city center (Čiháková & Frynta 1996), therefore, Kestrels are forced to hunt voles outside of the urbanized area.

Vole-eating raptors are mainly territorial, due to large energy requirements (Peery 2000). Many factors affect their home range size, especially food conditions (Village 1982, 1987), breeding

density (Bowman & Bird 1986, Leary et al. 1998), phase of breeding cycle (Sparks et al. 1994) and relatedness of individuals (Walls & Kenward 2001).

The Kestrel territory is defined as actively defended area, usually within a radius up 100 m from the nest (Cavé 1968). On the other hand, home ranges (~ whole activity ranges) can be several times larger than territories. In general, Kestrel home ranges are always larger than actively defended territories (Village 1990).

Common Kestrels maintain their territories during the breeding season (migratory populations) or throughout the whole year (resident populations, Village 1990), defending them from other Kestrels. Similarly to other falcons, Kestrel males provide most of the food for chicks (Cramp & Simmons 1980). Simultaneously, the males defend their territories more often and more vigorously than females (Wiklund & Village 1992). The hunting ranges of Kestrels may usually

surround the nest (Village 1990, Cavé 1968), thus inside of the home range. The size of territory and home range may decrease with the course of breeding season (Cavé 1968) and increase when density of *Microtus* spp. decreases (Village 1990). The hunting range overlap could be a common feature, depending on conditions, included individual factors (Village 1990). However, these results were obtained from farmland populations only; information about spatial activity of urban Kestrels is missing.

The hunting ranges of Kestrel males were studied in a small sized city of 40 km² (České Budějovice, Czech Republic) during the time of chick rearing. The Kestrels breed in the city center (continuous urbanized area), as well as on its periphery (mosaic of urban and ruderal habitats). Kestrels in České Budějovice hunt almost exclusively outside of the urbanized area and the common vole *Microtus arvalis* dominated the diet of their chicks (68–88% by numbers, 89–95% within biomass), even during low vole years (Fainová 2005).

Given this, males nesting in the city center seem to have two possibilities of dividing among one another their hunting ranges placed in the city peripheral area: 1) to invade the periphery hunting ranges of other males (cohabitation) or 2) to establish their own exclusive hunting ranges (partitioning). Our predictions are that: a) the hunting ranges of males from the city center are larger compared to those of periphery males and b) the hunting ranges of males from the city center overlap more with those of other males than hunting ranges of periphery males do.

MATERIAL AND METHODS

Study area and Kestrel population

The population of Kestrels was studied in České Budějovice (Southern Bohemia; 49°N, 14°E; 40 km²; 100 000 inhabitants; 250–300 m a.s.l.) during the breeding seasons 2002–2004. The Kestrels breed in loft-windows of old buildings, factories and churches. A minority of nests were found on trees or in nest boxes, attached to buildings. The population of Kestrels included ca 30–40 breeding pairs each year (Riegert & Fuchs 2004). The hunting grounds are mostly meadows (36%), cereals (35%) and ruderal areas (19%). The rest (10%) were composed of alfalfa, rape or cornfields. The proportion of habitats did not change markedly between years (less than 3% in any of them).

Vole trapping

Pitfall traps (100 plastic bottles with a cut neck and a 2 l capacity) were used each year, following methodology of Anděra & Horáček (1982). The traps were installed on 10 Kestrel hunting grounds (a trap line was composed of 10 traps per hunting ground, span 3 m) in the second half of July. The timing of trapping was determined by the approximate end of the breeding season, when the last Kestrel chicks were reared. This arrangement enabled us to synchronize the trappings among years, since the population hatching span between years also varied (see further). The reason of synchronization of the trapping dates were because the intra-year fluctuations in our area are unknown. The traps were filled with a 4% fusion of formaldehyde as a fixation agent and exposed for 17 days. The trap lines were placed in two types of vegetation cover: meadow (6 lines) and ruderal (4 lines). The vegetation cover of ruderals is not cut; meadows are usually cut at the end of July. The trapping effort was 1700 trap-nights per year. We caught 266 voles in the breeding seasons 2000–2005: 19 in 2000 (1.9 ind./trap line), 29 in 2001 (2.9 ind./trap line), 79 in 2002 (7.9 ind./trap line), 20 in 2003 (2.0 ind./trap line), 21 in 2004 (2.1 ind./trap line) and 98 in 2005 (9.8 ind./trap line). The years 2002 and 2005 seemed to be peak vole years, whereas 2000, 2003 and 2004 were low vole years.

Trapping and tagging of Kestrels

The Kestrels were trapped near nesting holes, using a fake Eagle Owl *Bubo bubo*, without using a tape-recorder (owl decoy induced attack). All the animals were trapped during the incubation stage. A mist-net with a 50 mm mesh was used. For the purpose of this study, only males were tagged since they provide most of the food for the chicks (Cramp & Simmons 1980). Although there were up to 40 pairs in the city, trapping was possible only at approximately 1/3 of all nests in the city. In total, 46 males were trapped (2002: 15, 2003: 20, 2004: 11). The males were equipped with either wing-tags (34) or transmitters (12). The wing tags (2 x 5 cm) were installed on the patagium using a nylon rod (Village 1982). One or two tags of different/same coloration were used. The transmitters were of a standard "back-pack" type (4.5 g, with a TW-4 battery with a lifespan of up to six month). Three-piece Yaggi aerial and wideband receiver AR-8000 were used for telemetry locations.

Hunting range assessment

A total of 34 Kestrel male hunting ranges were assessed (2002: 11, 2003: 12, 2004: 11). The distribution of males on the gradient from city center to its periphery was quite equal (Spearman rank correlation, $r_s = 0.28$, $p > 0.05$, $n = 8$ distance categories). Eight males were radio tagged. We included into analyses only results obtained from 1 male with 12 locations. All 34 males were checked at the nest with visual control during the rearing of chicks. Moreover, all of these males bred successfully. The number of locations for the other 12 excluded males was far below 10. This was caused either by failure of their breeding attempts (8) or they were non-breeding males caught at another male's nest hole (4). The number of locations varied between 12 and 38 (mean 19.1 ± 6.4), totalling 661 locations. We did not include locations of over-flying Kestrel males that did not stop on the hunting grounds. The locations of wing-tagged males were collected during observations on the hunting grounds.

Fights among individuals were recorded during 30–60 min observations on hunting grounds. This parallel project was realized in the years 2000–2005 (2000: 27 hours, 2001: 34 hours, 2002: 28 hours, 2003: 69 hours, 2004: 65 hours and 2005: 67 hours). All the observations took part during rainless days only.

Records were gathered from May to July during the time of chick rearing. The start of observations in each year was set by the first hatching of chicks (4 May 2002, 17 May 2003, 17 May 2004). The mean date \pm SD of hatching for the population was as follows: 2002 — 15 May \pm 7 days ($n = 10$), 2003 — 27 May \pm 6 days ($n = 10$) and 2004 — 2 June \pm 7 days ($n = 12$). Therefore, observations were continued until the last chick fledged (at least for six weeks). All locations determined by telemetry were verified with visual sightings, using a binocular 7 \times 50.

The hunting range area was calculated using the Minimum Convex Polygon Method (Ford & Myers 1981), excluding the nest site. The nest was excluded because of possible effect of "artificial" enlargement of hunting area of Kestrels from city center that do not hunt nearby its nest and just over fly urbanized area. The polygon was assessed using hunting sightings only. The city center was represented by the center of the "old-town", where also lies an approximate geographical centroid of the total urbanized area. We use the terms "periphery" or "city centre Kestrels" (or their modifications) within the text. This means

that particular Kestrels that breed close to periphery or center (centroid) of the gradient of urbanized area within the city are not two distinctive categories of males. Therefore, our dataset does not have a discrete distribution and both the terms may just approximate the real position of the nest. Hunting range overlap was expressed as a percentage of the shared area between two hunting ranges. The overlap was measured for all overlapping "couples" of males.

Statistical analyses

To control for a potential bias of the method used, ANOVA was computed to compare radio-tagged vs. wing-tagged males (Statsoft, Inc. 1996). Generalized Linear Models (GLM) with a relevant link function were used to analyze an influence of factors on hunting range parameters (McCullagh & Nelder 1989). Factors were incorporated using forward selection, according to Mallows's Cp-statistics (Mallows 1973). The factors included are mentioned for each model. Only three males were observed in more than one year, thus partially removing the effect of pseudoreplications. We used t-tests for comparisons of groups of radio/wing-tagged males, and Kruskal-Wallis test to compare inter-year differences in the hunting range size. Data on male distribution within urbanized area and behavioral data on fights were analyzed using Spearman rank correlations.

RESULTS

Hunting range size and observation method used

The number of locations (wing-tagged males: 19.7 ± 6.9 , $n = 26$; radio-tagged males: 17.1 ± 3.9 , $n = 8$, t-test, d.f. = 1, $t = 0.992$, $p = 0.334$) and the hunting ranges (wing-tagged males: 6.2 ± 6.1 km²; radio-tagged males: 9.4 ± 8.6 km², t-test, d.f. = 1, $t = -1.14$, $p = 0.265$) did not show any differences between the two groups of males.

Nest location and hunting range size

Hunting range size varied from 0.8 to 25.0 km² (7.2 ± 6.9 km²). The data unit for analysis was represented by an individual male's hunting range. The numbers of locations, distance of the nest from city center and vole abundance were included into the GLM model. The amount of urbanized area within a hunting range was used as a covariate. The hunting range size was not affected by either number of locations or

vole abundance. The inter-year differences in the hunting range size (medians for years; 2002: 2.8 km², 2003: 4.5 km², 2004: 5.0 km²) were not significant (Kruskal-Wallis median test, $H = 2.08$, $df = 2$, $p = 0.354$). The hunting range size was negatively correlated with the distance of the nest from the city center (Table 1, Fig. 1).

Nest location and hunting ranges spacing

Hunting ranges of “periphery males” usually overlapped each other less than 10% (Fig. 2). Some hunting ranges of “periphery males” showed great overlap (> 50%). However, these couples tended to enlarge one of these hunting ranges (Fig. 2). Hunting ranges of “city center males” often covered most of ranges (up to 100%) of “periphery males” (Fig. 2). Ranges of males from “city center” often showed great overlap (30–50%), but the shared space was mainly represented by urbanized area (Fig. 2).

There was usually a greater overlap among center males than among the periphery ones (Fig. 3). The overlap of two hunting ranges varied from 0.3 to 51.4% (mean $12.5 \pm 11.6\%$). The data unit for analysis represented the intersection between two overlapping hunting ranges.

The sum of nest distances from the city center, calculated for each two males with overlapping hunting ranges, and vole abundance were included into the GLM model. The sum of the distances for a couple of nests indicates the position of nests in the area of the city as follows: A minimal value shows that both nests are situated near the city centroid, while a maximal value indicates that both nests lie close to the city periphery pole of the gradient.

The sum of nest distances from the center negatively affected the extent of overlap between hunting ranges (Table 1, Fig. 3). Minimum values of hunting range overlap were typical for “couples” of periphery males, maximum for center ones. Vole abundance did not affect the extent of overlap between hunting ranges.

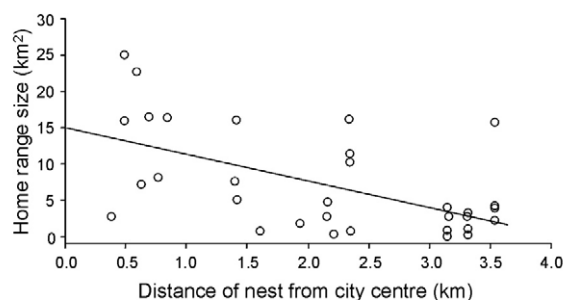


Fig. 1. Hunting range size and distance of the nest from the city center ($N = 34$).

Fights among hunting individuals

We recorded 91 fights among Kestrels on hunting grounds. The frequency of fights was negatively correlated with vole abundance (Spearman rank correlation, $r_s = -0.93$, $p < 0.05$, $n = 6$ years). We recorded both fights between tagged and non-tagged males (or pairs) from open landscape and also fights between two tagged males (one from periphery and the second from city center). The “intruders” were, as a rule, driven from the hunting ground (or territory) of defending pair.

DISCUSSION

Hunting range size

Although, both the methods used are adequate for studying hunting ranges, they can clearly differ in results obtained. While the data from radio-tracking are “real”, those from wing-tagging are dependent on actual position of the observer and what the observer can see (wing-tagged Kestrels were safely distinguished at distance less than 200 m approximately). Therefore, we compared these two datasets. The hunting ranges of radio-tagged males were distinctively larger than those of wing-tagged males, which was caused by a male’s nest location. Five radio-tagged males nested up to 2 km from the city centre and only three

Table 1. Statistical analyses of the home range parameters of urban Kestrel males from České Budějovice. GLM, forward factor selection, only factors with significant effect are included. * — covariate: urbanized area.

Dependent variable	N	Model type	Independent variable	% of explained variability	β	p
Home range size (km ²)*	34	Gamma	Distance of nest from center	32.2	-0.90	0.0004
Home range overlap (%)	94	Gamma	Distance of nests from center (sum)	3.9	-0.76	0.0351

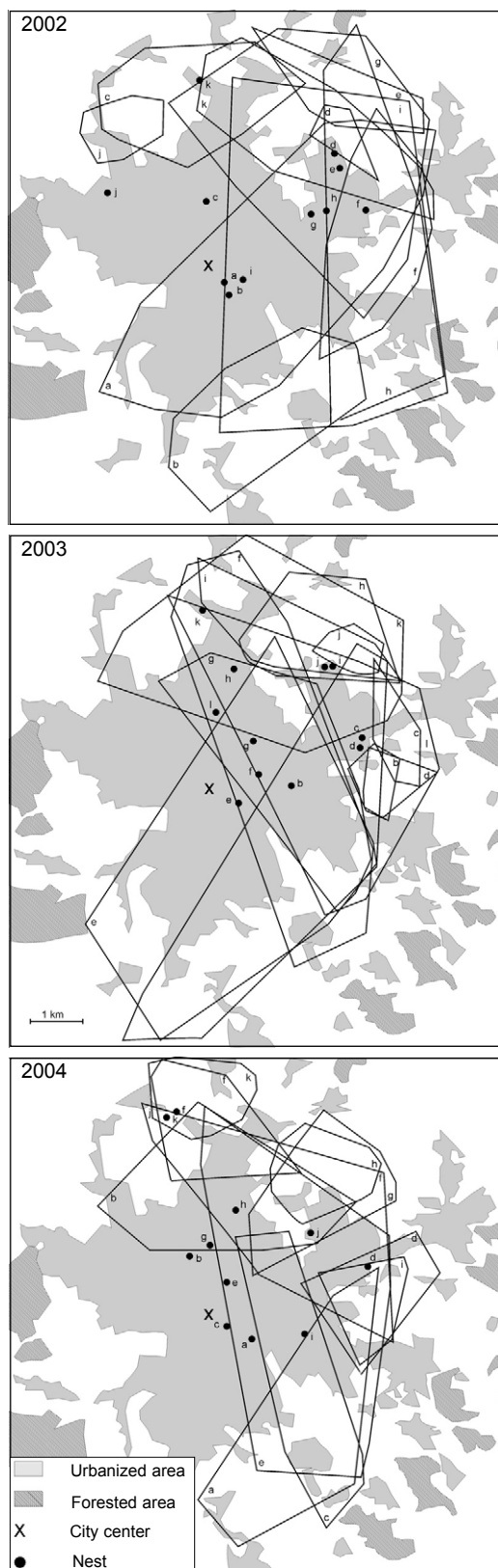


Fig. 2. The distribution of hunting ranges of Kestrel males from České Budějovice in the year 2002–2004.

radio-tagged males were from the city periphery. These results are comparable with those of Village (1982) who did not find significant differences in hunting range sizes between radio- and wing-tagged Kestrels. Unlike Village (1982), we did not find the relationship between number of locations and hunting range size.

Hunting range size and overlap

The results of the hunting range size and overlap analyses supported our first hypothesis: males from the center had larger hunting ranges than those from the periphery, even when the urbanized area was included into the analysis as a covariate. The hunting ranges of “males from the center” markedly overlapped with each other, as well as with most of those of “males from the city periphery”. This finding is evidence that only “periphery males” defend their hunting ranges located within the nest surroundings. The “males from the center” make incursions into the hunting ranges of the “periphery males”. It is difficult for males breeding in the city center to defend their hunting ranges, because they have to fly over urbanized areas before reaching their hunting ground. Thus, they can not patrol its hunting ground continually. At the same time, they interact with males that breed near the hunting grounds on the city periphery.

In spite that we did not include the nest site, the mean hunting range size of the Kestrel males in this study was higher than home ranges found in farmland habitats (1.1–5.7 km², Village 1982; 0.9 km², Mikeš 2003; 7.2 km² this study), probably because of different strategies used by males from the center. The home range size of Kestrels could be affected by vole abundance (Village 1982, Bowman & Bird 1986, Dunk & Cooper 1994), but we did not record any correlation between them. The correlation between vole abundance and hunting range was indicative only. Again, this might be due to the particular strategy of the center males. The males have similar area of their hunting range regardless of the vole abundance. The size of hunting range of “males from center” is rather determined by aggressive behaviour of “males from city periphery” and not by food availability. Moreover, we measured hunting ranges, and not home range area, since the nest site was excluded from hunting range. The decreased vole abundance was followed only by increased aggressive behaviour of Kestrels at hunting grounds. This result is in concordance with findings of Village (1990).

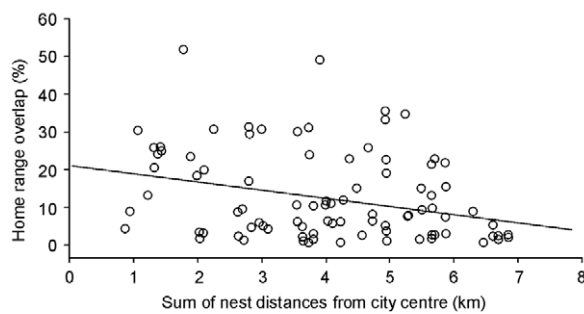


Fig. 3. The hunting range overlap for couples of nests, related to nest position ($N = 94$ couples).

Our results lead to the question of how the large hunting ranges of “center males” originated. They can visit only one or more hunting grounds per trip. In the first case, the male stays on the ground until the prey is caught. In the second case, if the male does not catch a prey within a particular time, it moves to another hunting ground. The recorded trips of some males (two examples in Fig. 4) and our behavioral data support the second hypothesis. The trip route could be more or less fixed, since males left the nest in a similar direction every day. Fixed daily routines in Kestrels were noted by Rijnsdorp et al. (1981). The changing of hunting grounds within one trip may be due to conflicts with local Kestrels. According to our observations, conflicts with both males and females were quite common. This was probably because the “intruder” male

passed the border of territory of periphery pairs, which also partially included hunting range of these Kestrels.

Disadvantageously, males of the city center spent much energy by flying to distant suitable hunting areas and by frequently changing their hunting grounds. Therefore, why do Kestrels nest in the city center? We provide two possible explanations. The nesting possibilities on the periphery could be limited or nest sites in the centre are of higher quality, for example safer sites from predators in the city center. Kestrel densities inside the cities are higher compared to city peripheries (i.e. Hudec et al. 1981, Darolová 1992, Plesník 1992, Salvati et al. 1999, Wassmer 2001). However, the results of this study may support both of the above mentioned hypotheses.

We conclude that Kestrels show partial cohabitation of periphery hunting grounds, but the inter-species aggression probably plays a key role for the use of these grounds. The males from the city centre have to change their hunting grounds because of aggressive attacks of periphery Kestrels. The evidence for cohabitation is indirectly given by great overlap among “central” and “periphery” ranges of males.

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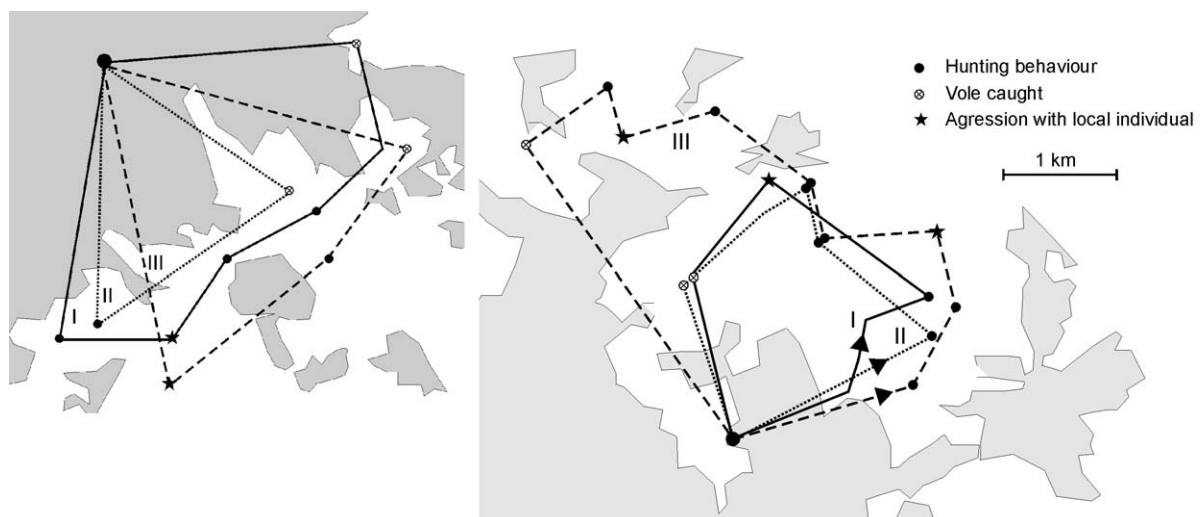


Fig. 4. Examples of particular routes in two males breeding near the center of the city (left) and half-way between city center and its periphery (right): left) 6.6.2003. Routes I (10:36–11:22), II (13:01–13:30) and III (16:05–17:56) finished by successful strike on the last hunting ground; right) 14.6.2002. Routes I (8:28–10:10), II (10:12–10:56) and III (11:10–15:05) finished by successful strike on the last hunting ground.

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STRESZCZENIE

[Sposób użytkowania terenów łowieckich przez miejskie pustułki w Czeskich Budziejowicach]

Pustułka jest jednym z nielicznych gatunków ptaków drapieżnych zasiedlających tereny miejskie. Poszczególne gniazda tych ptaków znajdują się zarówno w centrum miasta (obszar ciągłej zabudowy) jak i na obrzeżach (obszar mozaiki środowisk miejskich i ruderalnych). Badania prowadzono w Czeskich Budziejowicach gdzie liczebność tego drapieżnika sięga 30–40 par, w latach 2002–2004. Przedmiotem badań były zasięgi łowieckie 34 samców pustulek w okresie opieki nad pisklętami.

W celu oszacowania dostępności podstawowej zdobyczy pustulek — norników, co roku w obrębie 10 terytoriów łowieckich rozmieszczono 100 pułapek żywołownych. Pustułki chwymano w sąsiedztwie gniazd wykorzystując imitację pułchacza. Schwymane samce były znakowane z wykorzystaniem znaczków naskrzydłowych albo wyposażane w nadajniki telemetryczne. Sposób znakowania ptaka nie wpływał na uzyskiwane wyniki. Wielkość terytorium łowieckiego określano na podstawie 12–28 lokalizacji (z wyłączeniem stanowisk lęgowych) metodą Minimum Convex Polygon. Nakładanie się zasięgów określano jako procent wspólnie użytkowanego obszaru dwóch terytoriów.

Wielkość obszaru łowieckiego wahała się od 0.8 do 25 km² (śr. 7.2 ± 6.9 km²). Zasięg nie był zależny od liczby lokalizacji oraz dostępności ofiar. Stwierdzono natomiast negatywny związek między odległością do gniazda z centrum miasta (Tab. 1, Fig. 1). Nakładanie się terytoriów łowieckich wahało się między 0.3% a 51.4% (śr. $12.5 \pm 11.6\%$). Dostępność norników nie wpływała na stopień nakładania się terytoriów, natomiast najmniejsze wartości nakładania się były charakterystyczne dla "par" samców z terenów peryferyjnych, natomiast największe — dla samców gniazdujących w centrum miasta (Tab. 1, Fig. 2, 3). W oparciu o obserwacje zachowań samców gniazdujących w centrum miasta stwierdzono, że w razie

niepowodzenia przenoszą się na inne terytoria (Fig. 4).

Podczas badań stwierdzono, że samce z centrum miasta dokonują penetracji terytoriów łowieckich samców gniazdujących na peryferiach. Same nie mogą stale patrolować swych terenów łowieckich i wchodzą w interakcje z samcami/parami zajmującymi terytoria w sąsiedztwie terenów łowieckich. Pustułki wykazują częściowe współużytkowanie pozamiejskich terenów łowieckich, lecz konflikty między poszczególnymi osobnikami odgrywają prawdopodobnie znaczącą rolę w sposobie ich użytkowania. Samce z centrum miasta muszą często zmieniać miejsca polowań z uwagi na ataki osobników zasiedlający tereny peryferyjne.

