

Sex skewed kleptoparasitic exploitation of common kestrel *Falco tinnunculus*: the role of hunting costs to victims and tactics of kleptoparasites

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Abstract. Sex skewed kleptoparasitic exploitation of kestrel *Falco tinnunculus* was studied on foraging areas in south-east Poland. All kestrel prey subject to kleptoparasitism attempts were small mammals caught by kestrels hunting by hovering. Kleptoparasites attacked male kestrels more frequently than females. Males did not defend their prey as vigorously as females but males were more efficient at capturing further prey following loss of prey. Males also seemed to select habitats that facilitated more effective foraging which reduced costs of lost prey. Kleptoparasitism on kestrels was more successful by groups than by individual attackers.

Key words: Sex skewed kleptoparasitism, common kestrel, *Falco tinnunculus*, Poland, farmland

Introduction

Optimal foraging theory predicts that a forager should resort to kleptoparasitism when the net energy derived from this strategy exceeds the net energy gained from searching for food itself (Stephens & Krebs 1986, Aillock 1998). Kleptoparasitism is also considered as a strategy of dominance or competence, where dominant individuals benefit from the feeding success of subdominants by stealing food or by displacing other individuals from better quality feeding sites (Bautista et al. 1995, 1998).

Food piracy has been reported for a variety of bird species (Brockmann & Barnard 1979, Newton 1979, Gibbs & Gibbs 1987). Kleptoparasitism usually has been observed near nesting areas (Brockmann & Barnard 1979, Osorno et al. 1992, Negro et al. 1992, Vickery & Brooke 1994, Kitowski 2001a). However, it has also been observed at foraging areas (Brockmann & Barnard 1979, Buckley 1987, Temeles & Wellicome 1992, Kitowski 2003). Some parasitic birds may attack a particular host, while ignoring other birds. Such selective food piracy appears to be related to the age of the pirates and to the size of the host, sexual dimorphism in coloration and their relative abundance (Burger & Gochfeld 1981, Spear & Ainley 1993, Cummins 1995, Chavez-Ramirez 1995).

Numerous field observations indicate that the common kestrel *Falco tinnunculus* is frequently targeted by other birds performing kleptoparasitic attacks, though the species itself is also known to steal prey from other raptors (Schipper 1977, Brockmann & Barnard 1979, Shrubbs 1982, Village 1990). This paper presents the results of observations of sex-skewed kleptoparasitic exploitation of kestrels by various raptors and corvids foraging in south-east Poland.

Study Area and Methods

The research was carried out in meadows within a highly diverse agricultural landscape located near Chelm (triangle of villages: Kamen, Andrzejow, Kroczyn) in south-eastern Poland. My observation sessions spanned 15 May–25 July, 1997–1999. To avoid morning and evening mists, which were typical of the area, observations were conducted between 0700 and 1500 hrs. Three observers conducted 36 observation sessions, totalling 432 h. Observations included recording the behaviour of all birds within a radius of 1 km around the observers (3.14 km²). We recorded the following habitat types in the areas around observers: (1) regularly cut (intensive) meadows, (2) extensive meadows (meadows with high vegetation), (3) burnt meadows, (4) wasteland with high vegetation, (5) fields, (6) orchards, (7) settlements, (8) shrub coppices, and (9) other habitat types. Habitat types within the study area were mapped onto high-resolution aerial photos and their area was calculated with a digital planimeter. An electronic stop watch was used to estimate the duration of a particular behaviour. A 60 X telescope and 10 X 60 binoculars were used as observational tools. The duration of behavioral events was timed with an electronic stop-watch. Remnants of kestrel prey from 6 very often used plucking places were also collected.

From 1–4 common kestrel pairs nested annually near meadow borders and on cement plant infrastructure facilities. Further, 3–4 kestrel pairs nested each year in single poplars (*Populus* spp.) growing in the coppices that surrounded meadows. A relatively short distance separated meadows from calcareous peat-bog reserves, where 20–50 breeding pairs of Montagu's harrier *Circus pygargus* and 40–70 pairs of Marsh harrier *Circus aeruginosus* (B u c z e k & K e l l e r 1994, K i t o w s k i 2002, K i t o w s k i I., unpublished data) tended to nest each year. Meadows provided one of the basic foraging areas for harriers from the "Brzezno" and "Rozkosz" reserves. In the coppices and in-field tree stands located nearby and on the meadows, 3–4 pairs of common buzzards (*Buteo buteo*) are known to nest. In coppices, orchards, and meadows, 3–4 pairs of buzzards are known to nest. Magpies (*Pica pica*) in the area were observed regularly. Two breeding pairs of magpies nested in small shrub stands were, while another nest was found nearby. Also three active nests of hooded crow (*Corvus corone cornix*) were known from the study area.

Prey biomass was calculated using data found in B u s s e (1990) for birds and P u c e k (1984) for mammals. Chi-square tests with Yates correction were used to compare differences in frequencies, while Mann-Whitney U tests were used to compare medians (non-parametric data). Results are given as means \pm standard errors (F o w l e r & C o h e n 1992).

Results

Hunting success of hosts

I observed 342 attacks on prey by common kestrels during the study, of which 246 attacks were performed by males, and 96 by females. Males were successful in 88 (35.7%) attacks, whereas 26 (27%) female attacks were successful (Tables 1 and 2). Overall hunting success for observed kestrels was 33.3%, which was not different between sexes ($\chi^2 = 1.97$, $df=1$, N.S). Males also seemed to concentrate their foraging in intensive meadows, whereas females tended to use different meadow types more uniformly (Table 3). Small mammals (mainly voles *Microtus* sp.) were the primary prey captured by kestrels (Tables 4 and 5).

Table 1. Hunting techniques of male common kestrels.

Hunt techniques	All events		Successful event		χ^2 <i>df</i> = 1
	N	%N	N ₁	%N ₁	
Cruising	34	13.8	6	6.8	2.39, n.s
Hovering	182	74.0	78	88.6	7.24*
Perching	30	12.2	4	4.6	3.35, n.s
Total	246	100	88	100	–

$p < 0.007^*$

Harassment of hosts

During 114 prey captures by kestrels over the three year period, 39 (34.2%) were associated with kleptoparasitic attacks by other birds (Table 6), all prey involved being small mammals. Kleptoparasites attacked male kestrels more frequently than females, involving 41% of all prey caught by males, compared with only three (11.5%) of 26 prey captured by females, the difference being significant ($\chi^2 = 6.44$, *df* = 1, $P < 0.011$). Overall, kleptoparasites pirated 21 prey from male kestrels, whereas with females, prey was successfully pirated only once. The overall number ($n = 22$) of prey lost by both sexes constituted 19.3% ($n = 114$) of all the prey caught in the foraging area, and 61.1% ($n = 36$) of the targeted prey. Lost prey had a biomass of 440 g, which was 21.3% of the total biomass of prey captured on meadow habitats (Table 4). Kleptoparasites attacked the hosts on average for 37.1 ± 5.3 s (range: 3–122 s).

Table 2. Hunting techniques of female common kestrels.

Hunting techniques	All events		Successful event		χ^2 <i>df</i> = 1
	N	%N	N ₁	%N ₁	
Cruising	14	14.6	3	11.6	0.1, n.s.
Hovering	55	57.3	16	61.5	0.03, n.s
Perching	27	28.1	7	26.9	0.02, n.s
Total	96	100	26	100	–

Kleptoparasites and their prey stealing tactics

Corvids-Corvidae

Eleven attempts to steal prey from kestrels were made by hooded crows (*Corvus corone cornix*) (Table 6). Four such attacks were performed by single birds, the rest involved a group of 2–3 hooded crows. However, only one attempt by a single individual hooded crow was successful, while six of seven attempts by groups were successful. Attempts by individuals lasted an average 27.5 ± 8.6 s (range 17–53 s). In contrast, attempts by groups lasted on average 99.6 ± 10.1 s (range 46–122 s). The duration of parasitic attacks of kestrels by groups of hooded crows was longer than parasitic attacks by individual crows (Mann – Whitney U test: $U = 1$, $n_1 = 7$, $n_2 = 4$, $P < 0.05$).

Magpies attempted six parasitic attacks on kestrels (Table 6), with all observed cases happening near bushes which kestrels used for shelter after being attacked. Two individual and

one kleptoparasitic group act resulted kestrels dropping prey. Attempts by individual magpies (n = 4) lasted an average of 18.7 ± 1.9 s (range: 14–23 s). The duration of the two social attempts, with the participation of three and four individuals, respectively, lasted 33s and 41s (37.0 ± 4.0 s). After magpie groups were successful, individuals fought over prey. Kleptoparasitic attacks by magpies were not significantly longer than kleptoparasitic attacks by hooded crows (24.8 ± 4.2 s v.s 73.4 ± 13.0 s: Mann-Whitney U test: U =12, n₁ = 6, n₂ = 11, N.S). However, the absence of differences may be related to the small sample size. In general, kestrels were robbed by magpies less frequently than by other corvids. Magpies seemed to follow male kestrels to their plucking sites, and then consume prey remains after the kestrel left (n = 4).

For 41 s a group of three jackdaws *Corvus monedula* chased a kestrel until it dropped the prey onto a meadow (Table 6). One of these jackdaws consumed the stolen prey on the ground. Also, one kleptoparasitic attack by four rooks *Corvus frugilegus* who chased a kestrel for 57 seconds was recorded. Once the kestrel dropped the prey, it was first carried 40 m by one rook, and then taken by a second rook which ate the prey.

A different parasitic tactic was demonstrated by a raven *Corvus corax*. The bird circled over a kestrel eating small mammal prey on a small block of compressed hay for about 40 seconds. Then the raven landed on the kestrels' plucking place, which caused the falcon to flush and lose its prey. The prey was instantly consumed by the intruder. The observed interaction lasted only 3 seconds. This observation was unusual since ravens tended to compete for large carrion with marsh harriers (n=1), buzzards (n=2), or foxes *Vulpes vulpes* (n=1), as well as flocks of rooks (n=2).

Table 3. Frequency of hunting attempts by common kestrels on prey in relation to habitat type use for males and females.

Habitat type	Availability		Males			Females	
	%	N	%N	$\chi^2, df=1$	N ₁	%N ₁	$\chi^2, df=1$
Intensive meadows	47%	199	81.0	112.4***	34	34.5	5.06*
Extensive meadows	23%	6	2.4	59.4***	23	24.0	0.05, n.s
Outburnt meadows	7%	31	12.6	12.4***	29	30.2	74.6***
Wasteland	8%	1	0.4	–	4	4.2	2.18, n.s
Fields	6%	4	1.6	8.59**	4	4.2	0.71, n.s
Orchards	4%	2	0.8	–	1	1.0	–
Human settlement	2%	1	0.4	–	–	–	–
Shrub coppices	2%	1	0.4	–	–	–	–
Others	1%	1	0.4	–	1	1.0	–
Total	100%	246	100	–	96	100	–

p < 0.05*, p < 0.01**, p < 0.001***

Raptors

Kestrels with prey were also mobbed by Montagu's harriers (Table 6), which quickly approached the kestrel made one attempt to take the prey (small mammal) from the grip of the kestrel. Kleptoparasitic attacks by Montagu's harriers lasted 14–21 s, with an average of 17.6 ± 0.9 s (n = 7) for males and 27.7 ± 2.8 s (range 22–31 s, n=3) for females. While defending their

prey against one male and one female Montagu's harrier, kestrel females managed to protect their prey by transferring it from one foot to the other.

An interesting tactic of robbing kestrels was exhibited by two year old male Montagu's harriers. Four attacks, lasting on average of 20.5 ± 4.0 s (range: 12–33 s), which included chasing kestrels, was preceded each time by begging by the harriers that lasted on average 21.7 ± 5.1 s (range 9–36 s). Three of these attacks were successful (Table 6). Also male kestrels were observed unsuccessfully ($n = 3$) attempting to rob prey from female kestrels. These bouts lasted 21.3 ± 4.4 s (range: 14–29 s), and were characterized by cartwheel-like flights. Corvids mobbed kestrels (52.4 ± 9.2 s, range 3–122 s) longer than raptors (20.5 ± 1.3 s, range 12–31 s, Mann-Whitney U-test: $Z = -2.81$, $n_1 = 19$, $n_2 = 20$, $P < 0.005$). No cases of kleptoparasitic attacks were undertaken by mixed species groups. However, I did observe mobbing of kestrels (individual without prey) by flocks of mixed species of passerines ($n = 11$) and corvids ($n = 2$).

Table 4. Frequency and biomass of prey captured by kestrels.

Prey	Average biomass of prey type [g]	<i>N</i>	Biomass [g]	Biomass [%]
Small mammals	20	97	1940	94.0
Passerines	20.	6	120	5.8
Tettigonioidae	0.5	4	2	0.1
Small invertebrates	0.2	7	1.4	0.1
Total	–	114	2063.4	100

Kestrel behaviour responses following kleptoparasitism

Kestrels that lost their prey ($n = 22$) exhibited one of the following behavioural patterns: 1) one female and four males left the area of study and were no longer observed 2) The remaining males – victims of kleptoparasitic attacks ($n = 17$) caught prey within an average: 339 ± 43.5 s (range: 178–843 s) after the losing prey. It was significantly lower in comparison to females ($n = 14$) that restarted hunting after aggressive interactions, ground resting, prey consumption, etc. (average 1396.1 ± 69.6 s, range: 763–1539 s, Mann-Whitney U-test: $Z = -4.882$, $n_1 = 17$, $n_2 = 14$, $P < 0.001$). For all the other successful hunting sessions of kestrels, the initial moment of the hunting session was not known.

Table 5. Estimated prey biomass of kestrel prey at nine plucking sites.

Prey	Average biomass of prey type [g]	<i>N</i>	Biomass [g]	Biomass [%]
<i>Microtus arvalis</i>	20	33	660	89.1
Passerines	20	3	60	8.1
Small frogs	10	2	20	2.73
<i>Tettigonia viridissima</i>	0.5	1	0.5	0.07
Total	–	41	740.5 g	100

Table 6. Kleptoparasites of common kestrels. Asterisks means successful attacks.

Species of harasser	N	Individual kleptoparasitism	Rate of success	Social kleptoparasitism	Rate of success
<i>Corvus corone cornix</i>	11	4(1*)	0.25	7(6*)	0.86
<i>Pica pica</i>	6	4(2*)	0.5	2(1*)	0.5
<i>Corvus monedula</i>	1	–	–	1(1*)	1.0
<i>Corvus frugilegus</i>	1	–	–	1(1*)	1.0
<i>Corvus corax</i>	1	1(1*)	1.0	–	–
<i>Circus pygargus</i> (males)	7	7(4*)	0.57	–	–
<i>Circus pygargus</i> (females)	3	3(2*)	0.66	–	–
<i>Circus pygargus</i> (imm.)	4	4(3*)	0.75	–	–
<i>Circus aeruginosus</i> (males)	2	2(0*)	0	–	–
<i>Falco tinnunculus</i> (females)	3	3(0*)	0	–	–
Total	39	28(13*)	0.46	11(9*)	0.81

Discussion

All common kestrel prey that were the objects of kleptoparasitism attempts were small mammals which were caught by kestrels using a hovering hunting technique. There are several possible reasons for kleptoparasitism following a hover hunting technique. Firstly, hovering is the primary hunting technique for catching small mammals in small habitat patches (Mendelson & Jakšić 1989, Village 1990), whereas all the other hunting techniques exhibited by kestrels in southeast Poland are used to catch birds (Rijnsdorp et al. 1981, Pettifor 1990, Village 1990). Second, hovering allows a kleptoparasite to locate hunting kestrels very easily. The open nature of foraging area, meadows in this case, favours easy detection of hosts (Brockmann & Barnard 1979, Kitowski 2001a).

Results suggested that males did not defend their prey as strongly as females. Females evaded kleptoparasites longer and performed more activities protecting prey. Such behaviour by females helped limit mobber interactions and made their attacks more expensive and sometimes even dangerous, as it has been reported for other species of birds (Brockmann & Barnard 1979, Kitowski 2001b, Simmons & Mendelsohn 1993). On the other hand, the ease by which male kestrels lost prey to kleptoparasites suggests some reasons for this seemingly low level of prey defence. It is possible that male kestrels incur low hunting costs because they are efficient predators as evidenced by the rapid time to their next successful kill following loss of prey. Males also seemed to select habitats that facilitated more effective foraging because they used habitats with lower vegetation (Wakelley 1978, Collopy & Bildstein 1987, Baker & Brooks 1981, Preston 1990).

Magpies, in contrast to hooded crows, did not benefit as much from kleptoparasitic attacks on kestrels (63.6% vs. 50.0%). It is possible in my study area that the magpies' tactics of close following of kestrels was more beneficial for them. When magpies follow kestrels to check their plucking perches, they incur lower costs than aggressive flight attacks. Disturbance of kestrels when they are eating may also provoke flight and subsequent leaving of prey. The high density of raptors that attack kestrels and the observed relatively high number of magpies following the kestrels that check their plucking places, can suggest that permanent relationship between the observed birds had been established. Observations support earlier observations of similar interactions between foraging American kestrels *Falco sparverius* and magpies (Sarno 1989).

My research also showed that kleptoparasitism was more successful by groups than by individual attackers. This result confirmed many reports for birds that social kleptoparasitism is more successful than individual kleptoparasitism (Buckley 1987, Cummins 1995, Ratcliffe et al. 1997).

The results from farmland of south-eastern Poland are related to a reversal sexual dimorphism exhibited in common kestrels. Sexual dimorphism is important for parental roles (Newton 1979). Kestrels show a clear a division of labour between the sexes during the reproductive period. Males catch most of the food for their dependants from before the pre-laying period to the late nestling period, whereas females are mainly responsible for incubation and the care of nestlings. Females start hunting in the late nestling period (Village 1990). The females are larger than males, though the differences amounts to only 4% of the male wing chord. Females are heavier (about 19%) than males (Village 1990, Dijkstra et al. 1988). Sexual dimorphism is most pronounced in the plumage coloration. Males are blue – grey on the head, rump and tail and brick – red with brown spots on the back and scapulars. Females are mostly brownish with brown bars on the back and tail. The underparts of both sexes are pale. Both adult and yearling males vary in plumage coloration. Differences are most distinct in the brightness of tail and dorsal coloration and in the back – spots (Plokongas et al. 1994). This clear sexual dimorphism benefits males in the effective hunting of agile prey and benefits females in the defence of caught prey.

In conclusion, it is possible that sex biased kleptoparasitism, where male kestrels are more likely victims of successful attacks, may be the result of several factors. For example, it is possible that the striking sexual dimorphism of males may make them more conspicuous targets of attack. In addition, males appear not to defend their prey as vigorously as females, and males are more efficient at capturing more prey following loss of prey. On the other hand, kleptoparasites may optimise their tactics by using a variety of methods such as social attacks (corvids), prolonging chase sessions and alternating begging behaviour with attacking behaviour (immature Montagu's harriers).

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