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Source: Acta Ornithologica, 38(2) : 129-134

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.038.0210

ACTA ORNITHOLOGICA
Vol. 38 (2003) No. 2

Aerial hunting behaviour of the Lesser Kestrel *Falco naumanni* during the breeding season in Thessaly (Greece)

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Vlachos Ch., Bakaloudis D., Chatzinikos E., Papadopoulos Th., Tsalagas D. 2003. Aerial hunting behaviour of the Lesser Kestrel *Falco naumanni* during the breeding season in Thessaly (Greece). Acta Ornithol. 38: 129–134.

Abstract. We studied the foraging behaviour of Lesser Kestrels in agricultural habitats during the breeding season of 2000. The birds spent more time hunting in flight than perched. During 398 min. of observed aerial hunting, they spent 23.7% hovering, 14.4% hanging, 14.0% flapping, 41.2% gliding, and 6.7% soaring. The time spent on each type of aerial hunting behaviour depended on factors like breeding stage, time of day, wind speed, number of strikes, number of successful strikes, and the time spent hunting. The strike rate was 0.38 per min., the capture rate 0.10 per min. The capture rate depended on the type of hunting behaviour preceding the attack and was highest after the birds had been hovering.

Key words: Lesser Kestrel, *Falco naumanni*, hunting methods, strike rate, capture rate

Received — June 2003, accepted — Oct. 2003

INTRODUCTION

The Lesser Kestrel is a small, colonial raptor, associated with warm, open, arid steppe-like habitats in flat or slightly undulating terrain. In many areas of its range, the Lesser Kestrel breeds in association with man, using buildings for nesting and agricultural habitats for hunting. Once considered one of the most numerous birds of prey in Europe (Eakle 1994), it has shown extensive population declines over large portions of its western Palearctic range since the 1960s (Bijleveld 1974, Cramp & Simmons 1980, Biber 1996). Recently, the Lesser Kestrel has received considerable conservation attention, and is now considered to be vulnerable in Europe (Hagemeijer & Blair 1997). Reasons for decline throughout its range include the reduction of favourable nesting habitats (restoration and/or demolition of old buildings), and the intensification in agricultural practices (Donazar et al. 1993, Biber 1996).

Although the reduction of suitable foraging habitat through land-use changes is recognised as the major factor causing Lesser Kestrel population declines (Hagemeijer & Blair 1997), only a few efforts have been made to study foraging habitat selection by Lesser Kestrels in southern Spain (Donazar et al. 1993). However, no quantitative information is available in the literature on hunting success or foraging behaviour of the Lesser Kestrel. Such information would greatly facilitate our understanding of Lesser Kestrel foraging ecology, which in turn could help land and resource managers to develop and manage certain foraging habitats to better meet the kestrel's needs (Newton 1979).

Our objectives were: 1) identify and quantify the aerial hunting behaviour of Lesser Kestrels, 2) to estimate hunting success, and 3) to assess differences between hunting methods.

STUDY AREA

The study area was located near the village of Megalo Monastiri (39°41′N, 22° 58′E) and surrounding region (50–180 m a.s.l.), where more than 100 pairs of Lesser Kestrels are known to breed. This small village is situated at the southeastern part of the Larisa Plain in central Thessaly, Greece on the edge of hilly terrain surrounded by grasslands and non-intensive agricultural land. Dominant crops are cereals followed by cotton and almond orchards. Agricultural practices have changed little over the past decades.

METHODS

Data were collected from May to mid-July 2000 during the incubation, brooding and post-fledging periods. The study area was classified into three main habitat types: cereals, grasslands, and cotton fields. Observation days were divided into three periods: morning (06:00–11:00), midday (11:00–16:00), and afternoon (16:00–19:30) (all local time). Data were collected during 2-day visits conducted at 15-day intervals, and included observations in all habitat types. Observation were carried out during each time period in an equal ratio to avoid time of day effects. Each habitat type was visited during one of the three time periods, with a total of 18 visits per habitat during the study.

Three sequential components of Lesser Kestrel foraging behaviour (modified from Remsen & Robinson 1990) were analysed, including: 1) foraging site — the general location and specific characteristics, 2) search or foraging — movements leading up to sighting of prey, and 3) strike — movements directed at a prey item (Rudolph 1982). Using instantaneous sampling methods (Martin & Bateson 1993, Lehner 1996), the frequency of hunting methods (hovering, hanging, flapping, gliding, and soaring) was recorded. Focal individuals were located at random and followed for 3 min. periods, recording hunting sequences every 10 sec. Time spent hunting was recorded from the first sighting of a Lesser Kestrel until it disappeared or completion of the 3 min. observation period. Successful hunting time (time spent hunting which led to a kill) was recorded from the first sighting of a Lesser Kestrel until a successful strike or the time between two strikes when the second was successful. Hunting Lesser Kestrels were classified as those birds that frequently hovered and searched the ground. Individual Lesser Kestrels that changed habitat types during the same observation period were excluded from our analysis.

The use of vantage points with a good view, and the high number of hunting birds, minimized the possibility of observing the same individual twice. For each hunting individual we recorded date, sex, location, time of day, wind velocity, wind direction, cloud cover, habitat type, and when possible, prey type captured. The main prey caught by Lesser Kestrels were arthropods, but on a few occasions small mammals were observed. Strike rate (number of strikes occurring per min. spent hunting), capture rate (number of prey items caught per min. spent hunting), strike success (proportion of successful strikes), and other parameters were calculated. As a full strikes was defined dives ended on the ground, while half strikes — dives abandoned before landing. All observations were made by two people using 10 × 40 binoculars, a wind speed counter, and a beeper.

A general linear model (GLM) was used to test whether a particular hunting behaviour was affected by stage of breeding season (ST), period of the day (DT), wind speed (WS), number of strikes (NoS), number of successful strikes (NoSS), or time spent hunting (TH). Percentage of time spent hunting by behaviour mode was arcsine transformed (Zar 1996) and used as the response variable in the GLM. WS and TH were included as covariates, whereas ST, DT, NoS and NoSS were included as factors in the GLM.

All statistical analyses (ANOVA, Kruskal-Wallis test, GLM, Chi-square test) were performed using the Minitab statistical package at the 0.05 significance level.

RESULTS

Hunting behaviour and methods

In 398-min. of observation, we recorded the following hunting behaviours — hovering (23.7%), hanging (14.4%), flapping (14.0%), gliding (41.2%), and soaring (6.7%). The overall strike rate was 0.38 and it was dependent on the type of hunting method employed ($\chi^2 = 32.29$, df = 4, $p < 0.001$). It was highest when Lesser Kestrels hovered, followed by hanging, gliding, flapping, and soaring (Table 1).

The proportion of Lesser Kestrels observed diving depended on the dominant hunting method used and was highest in hovering and hanging ($\chi^2 = 48.30$, df = 4, $p < 0.001$).

The average length of the time spent hunting by Lesser Kestrels was not affected by time of day or sex. In contrast, it was strongly affected by breeding season phase ($F_{2,235} = 3.73$, $p = 0.025$), num-

Table 1. Hunting behaviours employed by Lesser Kestrels. CRS — NoSFS/TSH, %SS — NoSFS/NoS, %S — NoSFS/HOD, %US — (HOD – NoSFS)/HOD, %POD — HOD/HLKs.

Parameters	Aerial hunting behaviour					Total
	Hovering	Hanging	Flapping	Gliding	Soaring	
Time spent hunting (TH) min.	94´20´´	57´30´´	55´40´´	164´10´´	26´50´´	398´30´´
Time spent for successful hunting (TSH) min.	17´20´´	7´00´´	4´30´´	8´50´´	0	37´40´´
Number of hunting birds (NHLKs)	63	19	24	119	13	238
Hunting birds observed diving (HOD)	52	13	8	45	1	119
Number of strikes (NoS)	69	19	15	47	0	150
Number of half strikes (NoHS)	10	2	1	13	0	26
Number of full strikes (NoFS)	59	17	14	34	0	124
Number of successful full strikes (NoSFS)	23	4	4	8	0	39
Strike rate (NoS/TH)	0.73	0.33	0.27	0.29	—	0.38
Capture rate (NoSFS/TH)	0.25	0.07	0.07	0.05	—	0.10
Capture rate of successful birds (CRS)	1.35	0.57	1.00	0.89	—	1.05
% of strike success (SS)	33.3	21.1	26.7	17.0	—	26.0
% of successful birds which diving (S)	44.2	30.8	50.0	17.8	0	32.8
% of unsuccessful birds which diving (US)	55.8	69.2	50.0	82.2	100	67.2
% of birds observed diving (POD)	82.5	68.4	33.3	37.8	7.7	50.0

ber of strikes ($F_{4,\ 233}$ = 3.18, p = 0.014), and number of successful strikes ($F_{1,\ 236}$ = 24.49, p < 0.001). The average length of time spent hunting by Lesser Kestrels during the incubation period was 117.4 sec (SD = 53.8 sec), which was longer than the average length of the time spent hunting during the brooding and post-fledging period (mean = 95.8 sec, SD = 52.6 sec and mean = 95.2 sec, SD = 47.3 sec, respectively). Also, the average length of the time spent hunting was 88.5 sec (SD = 56.4 sec) when one strike was performed, 118.9 sec (SD = 45.2 sec) for two strikes, and 105.1 sec (SD = 47.4 sec) for Lesser Kestrels with no strikes. In some cases we observed 3-4 strikes during the same hunting effort.

Similar results were found for the average length of the time spent hunting in relation to successful strikes. Average hunting time was 64.6 sec (SD = 49.8 sec) when Lesser Kestrels had one successful strike and 107.4 sec (SD = 49.3 sec) when unsuccessful. Also, an association was found between the length of the time spent hunting and type of strike ($F_{3,\ 234}$ = 4.96, p = 0.002). The average time spent hunting from first sighting until full strike was 87.8 sec (SD = 54.6 sec, n = 97), and it was significantly shorter than the average length of time spent hunting from first sighting until half strike (mean = 128.7 sec, n = 15). Average length of time spent hunting from first sighting until a hunting sequence without a strike or with a sequence of mixed strikes (full and half) was 105.1 sec (SD = 47.4 sec, n = 119) and 134.3 sec (SD = 35.1 sec, n = 7) respectively, but not significantly different.

GLM analysis (Table 2) revealed that hunting time spent hovering (p < 0.001) or hanging (p = 0.013) gradually decreased as the breeding season progressed, while gliding increased (p = 0.01). Period of day seems to have a negative effect on percent time hovering (p = 0.004) or soaring

Table 2. Coefficients from GLM analysis using stage of breeding season (ST), period of day (DT), wind speed (WS), number of strikes (NoS), number of successful strikes (NoSS), and time of hunting (TH) as explanatory variables and percent of time spent in each hunting behaviour by Lesser Kestrels as the response variable. *p < 0.05, **p < 0.01, ***p < 0.001.

Hunting behaviour	ST	DT	WS	NoS	NoSS	TH
Hovering	-5.018***	-2.331**	-0.5387***	9.641**	27.741***	—
Hanging	-4.89*	3.403**	0.928***	4.226**	—	0.0645***
Flapping	—	—	—	1.224*	-6.993**	—
Gliding	3.352**	1.224*	0.0277*	-7.67**	-16.266*	—
Soaring	—	-2.263**	-0.3093**	-4.841***	—	0.06045***

($p = 0.008$), and a positive effect on percent time hanging ($p = 0.006$) or gliding ($p = 0.035$). Lesser Kestrels gradually decreased the percent time hunting by hovering or soaring and gradually increased the percent time hunting by hanging or gliding as the day progressed from morning to afternoon.

Percent time hovering and soaring was inversely correlated with wind speed ($p < 0.001$ and $p = 0.005$, respectively). Opposite results were found for percent time hanging or gliding which were positively correlated with wind speed ($p < 0.001$ and $p = 0.041$, respectively).

Percent time hovering, hanging and flapping increased ($p = 0.003$, $p = 0.003$ and $p = 0.014$ respectively), while percent time gliding and soaring decreased ($p = 0.005$ and $p < 0.001$, respectively), as the number of strikes increased. Successful strikes were negatively associated with flapping ($p = 0.002$) and gliding ($p = 0.02$) and positively associated with hovering ($p < 0.001$). Moreover, a positive correlation was found between hunting time and percent time hanging ($p = 0.001$) and soaring ($p < 0.001$) (Table 2).

Hunting success

A total of 238 Lesser Kestrels were observed hunting of which 119 (50%) were seen diving. We observed 150 strikes of which 124 (82.7%) were full (dives that ended on the ground) and 26 (17.3%) were half (dives abandoned before landing). Of the 124 full strikes observed, 39 (31.5%) were successful. Strike rate was 0.38 strikes per min. and capture rate was 0.10 successful strikes per min. (Table 1).

Capture rate depended on the hunting behaviour preceding the strike ($\chi^2 = 23.66$, df = 4, $p < 0.001$). Capture rate was highest for hovering, followed by flapping, hanging, gliding, and soaring. In contrast, capture rate for successful Lesser Kestrels was not associated with the hunting behaviour preceding the strike ($\chi^2 = 1.73$, df = 3, $p = 0.63$).

The proportion of successful Lesser Kestrels observed diving was 32.8%. The proportion of Lesser Kestrels observed diving which successfully captured prey differed significantly among aerial hunting methods preceding the capture ($\chi^2 = 8.75$, df = 3, $p = 0.033$). That is, flapping resulted in a lower proportion of successful kestrels observed diving than hovering, hanging, gliding, and soaring.

The average time spent hunting which lead to a kill did not differ among the periods of day or between sexes. However, this time differed significantly with breeding stage, which gradually decreased from incubation to fledging ($F_{2,235} = 4.70$, $p = 0.01$).

Finally, the average time that successful Lesser Kestrels spent hunting over the three habitat types differed significantly (Kruskal-Wallis test: H = 7.74, df = 2, $p = 0.021$). Time spent hunting which lead to a kill was lower over grasslands (mean = 3.1 sec, SD = 9.81 sec, n = 108) and cotton fields (mean = 4.2 sec, SD = 16.5 sec, n = 26) than over cereals (mean = 17.5 sec, SD = 40.6 sec, n = 104). During our study grasslands were at the end of seed formation and drying, while cotton was growing with scarce vegetative cover. In contrast, cereals were close to harvesting and were the densest vegetative habitat type in the area. However, the mean density of grasshoppers in grasslands (mean = 4.68, SD = 4.34 insects/m^2, n = 40 plots) was significantly higher than in cereals (mean = 2.38, SD = 2.4 insects/m^2, n = 45 plots) and cotton fields (mean = 1.39, SD = 1.63 insects/m^2, n = 25 plots, $F_{2, 107} = 9.89$, $p < 0.001$, Vlachos et al. 2003).

DISCUSSION

Lesser Kestrels are known to hunt either from a perch or from the air. A shortage of suitable perch sites for hunting, which has been observed in the study area, may affect the prevalence (unless perching did not occur at all) of aerial hunting behaviour as has also been observed in Spain (Donazar et al. 1993). Although, no data were collected outside the reproductive season, our observations suggest that some variation in hunting behaviour does occur. Lesser Kestrels were observed employing five aerial hunting behaviours (gliding, hovering, hanging, flapping, and soaring) during the study, with soaring used proportionally less often because it is likely not a very effective way of searching for invertebrates (grasshoppers and field-crickets) on the ground (Village 1990).

Aerial hunting is energetically more expensive but has the advantage that many suitable habitat patches can be covered in a short period of time and more prey encountered (Wakeley 1978, Rudolph 1982, Village 1983). Aerial hunting is the main foraging mode employed by Lesser Kestrels during the reproductive season which allows the birds to maximise their daily energy gain by preferring the high cost-high yield technique (Rudolph 1982, Masman & Klaassen 1987, Masman et al. 1988). Gliding was found to be used more often because of the hilly terrain of the study area where Lesser Kestrels can make use of updrafts, reducing the energetic costs of hunting (Videler et al. 1983).

The use of different hunting methods appears to be strongly associated with wind velocity. On calm days with low wind speed, Lesser Kestrels tended to hunt mainly by hovering and soaring. Barnard (1986) reported the same for the morphometrically similar Rock Kestrel *F. tinnunculus rupicolus* in South Africa. On windy days Lesser Kestrels hunted more frequently by hanging, which is energetically less expensive than hovering. Similar findings have also been reported for Rock Kestrels, Jackal Buzzards *Buteo rufofuscus*, Black-shouldered Kites *Elanus caeruleus* (Barnard 1986), and Short-toed Eagles *Circaetus gallicus* (Bakaloudis 2000). Therefore, Lesser Kestrels probably compensate these high cost hunting methods (hovering, flapping, and hanging), with a higher number of strikes and successful strikes (Table 2) and increased capture rate (Table 1).

As the breeding season progressed, time spent hovering gradually decreased while time spent hanging and gliding increased. Although we expected hovering to be the dominant hunting method employed during the nestling period (Rudolph 1982, Village 1983), the change in hunting behaviour during the late breeding season could be explained by the entry of females into our sample, which hover less than the males (Cade 1982), or by higher hunting efficiency (time spent hunting leading to kill). Furthermore, as the period of the day progressed from the morning to afternoon, Lesser Kestrels spent more time hanging and less time hovering. Relationships between time of day and hunting method were probably associated with increased wind speed (causing updrafts) and prey availability (Barnard 1986).

Hunting efficiency variations among stages of the breeding season were probably affected by insect availability as well as vegetation cover (Baker & Brooks 1981, Bechard 1982). Lesser Kestrels hunted more efficiently over grasslands and cotton fields with scarce cover, making prey more accessible (Donazar et al. 1993, Bakaloudis 2000), and less efficiently over cereals with dense vegetative cover which reduced prey visibility and accessibility (Bechard 1982, Toland 1987).

Our results seem to confirm that Lesser Kestrels adjust their aerial hunting methods according to wind velocity during the breeding season in ways that can compensate the high cost-high yields with the most profitable habitat type.

ACKNOWLEDGEMENTS

We are most grateful to Dr. A. Wuczyński, and anonymous referee for their useful suggestions on an earlier draft of the manuscript. We also thank W. L. Eakle for his constructive comments on the manuscript and improvements to our English.

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STRESZCZENIE

[Zachowania łowieckie pustułeczki w okresie lęgowym]

Badania prowadzono od maja do połowy lipca 2000 r. w okolicach Megalo Monastiri (centralna Tessalia, Grecja), gdzie populacja pustułeczek osiąga liczebność ponad 100 par. Obserwacje prowadzono trzykrotnie w ciągu dnia: rano (06.00–11.00), w południe (11.00–16.00) i wieczorem (16.00–19.30) na trzech typach powierzchni badawczych — porośniętych zbożem, na łąkach i uprawach bawełny. Dane gromadzono w czasie dwudniowych badań prowadzonych co 15 dni. Każdy typ powierzchni wizytowano w sumie 18 razy. Analizowano trzy składowe zachowań łowieckich pustułeczki: stanowisko łowieckie, poszukiwanie i konsumpcja zdobyczy, atak na zdobycz. Określano także frekwencję występowania poszczególnych metod łowieckich (krążenie, zawisanie, szybowanie, lot aktywny, ślizgowy). Poszczególne osobniki były wybierane przypadkowo i śledzone przez okres 3 min.; w tym czasie zachowanie ptaka rejestrowano co 10 s.

Podczas 398 minut obserwacji stwierdzono, że lot ślizgowy zajmuje pustułeczkom 41.2% czasu, krążenie — 23.7%, zawisanie — 14.4%, lot aktywny — 14% a szybowanie — 6.7%. Współczynnik ataków wyniósł średnio 0.38/min. i był zależny od zastosowanej metody polowania. Najwyższe wartości osiągał podczas krążenia (Tab. 1). Średni czas trwania łowów pustułeczki nie był związany z porą dnia bądź płcią obserwowanego ptaka, zależał jednak od zaawansowania sezonu lęgowego, liczby ataków i liczby ataków zakończonych sukcesem. Czas spędzany przez pustułeczki na krążeniu i zawisaniu zmieniał się w czasie sezonu, zależał także od pory dnia (Tab. 2).

Spośród 150 obserwowanych ataków 82.7% kończyło się wylądowaniem ptaka na ziemi (full strike), 17.3% zostało przerwanych (half strike). 31.5% ataków, podczas których pustułeczka lądowała na ziemi kończyło się sukcesem. Współczynnik chwytania (atak zakończony sukcesem/min.) wyniósł 0.1.

T. Cofta