



Ecological and social factors affecting the occurrence of kleptoparasitism in two recently established sympatric breeding falcons

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Abstract

Co-occurrence of ecologically similar species can lead to direct agonistic interactions, including kleptoparasitism, where one individual consumes trophic resources acquired by another. We documented facultative kleptoparasitism in two similarly-sized raptors, the lesser kestrel (*Falco naumanni*) and the red-footed falcon (*Falco vespertinus*). These two species currently co-occur in Northern Italy due to recent range shifts influenced by climate and land-use changes. Multi-year focal observations revealed that single or multiple red-footed falcons were associated with 72% of foraging groups of lesser kestrels. Red-footed falcons initiated kleptoparasitic attacks on lesser kestrels in 46% of foraging group observations, with a success rate of 34%. Attacks were more likely when the prey capture rate (i.e. a proxy of foraging efficiency) of lesser kestrels was high. Red-footed falcons were more successful in stealing prey when the food items carried by lesser kestrels were larger, and kleptoparasitic attacks by groups of red-footed falcons had a higher success rate than attacks by singletons. Overall, we propose that such frequent kleptoparasitic events, which have never been previously documented in these two species, may have emerged as a consequence of their recently established co-occurrence. Kleptoparasitism could reduce the foraging efficiency and fitness of lesser kestrels, potentially leading to broader ecological consequences, such as population declines or range shifts. These findings highlight how species redistributions associated with global changes may lead to novel interspecific interactions with unforeseen ecological implications.

Significance statement

Species modifying their distribution due to environmental changes can colonize new regions, where they may establish novel interspecific interactions with local ecologically similar species or among themselves. This is the case for the recent co-occurrence between two raptors in Northern Italy, the lesser kestrel and the red-footed falcon. Notably, we found that co-occurrence is strongly characterized by systematic kleptoparasitism by red-footed falcons on lesser kestrels, and that attacks were more successful when lesser kestrels carried larger prey or involved multiple attackers. Our findings suggest that novel behavioral interactions following natural species redistributions may influence ecological dynamics.

Keywords Behavioral interference · Interspecific competition · Optimal foraging · Global changes · Raptors

Introduction

Stealing a captured food item from another individual of a different species, i.e. interspecific foraging kleptoparasitism, can be advantageous when the benefits of stolen food exceed the aggressor's effort and self-foraging costs (Thompson 1986; St. Clair et al. 2001). Kleptoparasitism can be highly selective, with attackers targeting only the most profitable

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victims (i.e. smaller species, vulnerable individuals) (Ridley and Child 2009; Marchowski and Neubauer 2019), in accordance with optimal foraging theory (Pyke 1984). Kleptoparasitism is indeed widespread (see Cangialosi 1990; Grimm and Klinge 1996; Sivinski et al. 1999; Cooper and Pérez-Mellado 2003; Brown et al. 2004; Iyengar 2008), though it appears to be most frequently observed among birds (Brockmann and Barnard 1979). Altricial bird species are susceptible to kleptoparasitism particularly during offspring-rearing, when parents behave as central-place foragers and transport food predictably from foraging areas to nest sites (St. Clair et al. 2001; García et al. 2010; Senzaki et al. 2014). Prey quality plays a major role in affecting kleptoparasitic attacks, promoting this behavior especially when food items are large or energy-rich (García et al. 2010; Marchowski and Neubauer 2019; Busniuk et al. 2020). Adverse environmental conditions, such as inclement weather, can result in diminished visibility and decreased prey activity, thereby fostering facultative kleptoparasitism (St. Clair et al. 2001).

Among birds, colonial breeders are often the preferred victims of facultative kleptoparasites, since high densities of potential victims may provide higher opportunities for kleptoparasitic behavior (Brockmann and Barnard 1979; Iyengar 2008). A classic example involves mixed-species seabird colonies, with kleptoparasitic gulls, skuas and frigatebirds frequently targeting relatively smaller species such as terns, puffins, auks, and boobies (e.g. Andersson 1976; Le Corre and Jouventin 1997; Schreiber and Burger 2001; St. Clair et al. 2001; Senzaki et al. 2014; Gaglio et al. 2018). These larger aggressors feed opportunistically and live in open environments where they can readily locate potential victims carrying food (Paulson 1985).

Although less frequently reported, facultative interspecific kleptoparasitism can also occur systematically or occasionally among species other than seabirds, such as ducks, rails, storks, corvids and other passerines (e.g. Amat and Soriguer 1984; Gonzalez 1996; Ridley and Child 2009; Marchowski and Neubauer 2019; but see Brockmann and Barnard 1979). Interspecific kleptoparasitism involving raptors as aggressors is poorly documented (e.g. Heredia and Clark 1984; Temeles 1990; Temeles and Wellicome 1992; Zuberogoitia et al. 2002; Siverio et al. 2008; Danko 2012; Baladrón and Pretelli 2013; for a review see Brockman and Barnard 1979; see also Negro et al. 1992 for a case of intraspecific kleptoparasitism). Except for bald eagles (*Haliaeetus leucocephalus*), which frequently kleptoparasitize other birds of prey during winter (Jorde and Lingle 1988; Dekker and Drever 2015), interspecific foraging kleptoparasitism

seems however rarely employed as a systematic foraging strategy by raptors. One possible explanation lies in the fact that raptors are top predators with specialized prey-capturing adaptations, while gulls and corvids are generalist, adapted to opportunistic scavenging and theft as an ecological strategy.

Anthropogenic global changes are currently reshaping animal communities (Clavero et al. 2011; Stephens et al. 2016), and some species are expanding their ranges and colonizing new areas (i.e. “newcomers”) (Beddall 1963; Holtmeier 2015), leading to new ecological interactions with pre-existing species and/or among other “newcomers” (Case and Gilpin 1974; Grether et al. 2013; Brambilla et al. 2020). Here we describe the systematic occurrence of kleptoparasitic interactions between two “newcomer” diurnal raptor species in a region of Northern Italy (Po Plain), the red-footed falcon (*Falco tinnunculus*) and the lesser kestrel (*Falco naumanni*), and investigate the ecological and social factors associated with its occurrence and success rate. Both species have recently (early 2000s) colonized the area, likely due to rapidly changing climatic conditions and land-use (Berlusconi et al. 2022; Morganti et al. 2017). This is the only region of their European distribution ranges where they are known to breed in sympatry (Keller et al. 2020). These two “newcomers” have similar ecological requirements, which could have promoted the emergence of kleptoparasitism as a novel form of ecological direct interaction. To the best of our knowledge, kleptoparasitic events between these two taxa have never previously documented, neither in Europe nor in other Asian regions where the two species have overlapping geographical ranges (Del Hoyo 2020).

We conducted observations of foraging lesser kestrel groups aiming to assess the frequency and success of kleptoparasitic events by red-footed falcons. We hypothesized that red-footed falcons would preferentially target lesser kestrels under specific ecological conditions (e.g. larger lesser kestrel groups, early morning, inclement weather, on low-height vegetation crops, high lesser kestrel foraging efficiency). We also predicted that red-footed falcons would increase their kleptoparasitic efforts (and therefore their success rate) when targeting lesser kestrels carrying larger (i.e. more profitable) prey, those that consume their food nearby the foraging areas (rather than rapidly escaping the foraging area to bring food to their nest at the colony), and those that had a milder defence behavior (i.e. emitting fewer alarm calls). Additionally, we anticipated that red-footed falcons would maximize their attack success when two or more kleptoparasites targeted the same victim together.

Materials and methods

Study species and area

The lesser kestrel and red-footed falcon share similar sizes (body mass approximately 130–150 g), the red-footed falcon being on average slightly (approximately 3%) longer-winged than the lesser kestrel (Storchová and Hořák 2018). European populations of the two species show different migratory patterns, the lesser kestrel wintering in the Sahelian belt (Sarà et al. 2019) and the red-footed falcon in Equatorial and Southern Africa (Palatitz et al. 2018). The study was conducted in the central-eastern Po Plain, Northern Italy (45.0°N, 11.5°E) across an area extending over approximately 4,000 km² (Fig. 1). This region, characterized by a Mediterranean sub-continental climate, features predominantly cultivated landscapes (about 80% land

use). Key crops include alfalfa (*Medicago sativa*), the so-called “winter cereals” (mainly *Triticum* and *Hordeum* genera), and irrigated summer crops like maize and soybean (Regione Emilia-Romagna 2009; Costantini et al. 2013). European lesser kestrel populations are mainly distributed in the Mediterranean region (below 40°N), while the European red-footed falcon’s range is limited to the Balkans and Eastern Europe (east of 22°E). In the study area, lesser kestrels breed mainly in colonies in abandoned farmhouses (2–12 pairs), while red-footed falcons breed singly or in loose colonies (up to 20 pairs) in trees, relying on old corvid nests. Both species thrive in open habitats like pseudo-steppes, semi-natural grasslands and agricultural landscapes with extensive grasslands and cereal crops (Morganti et al. 2021; Berlusconi et al. 2022; Lardelli et al. 2022), primarily targeting harvested cereals or mown crops for prey (AB, unpubl. data).

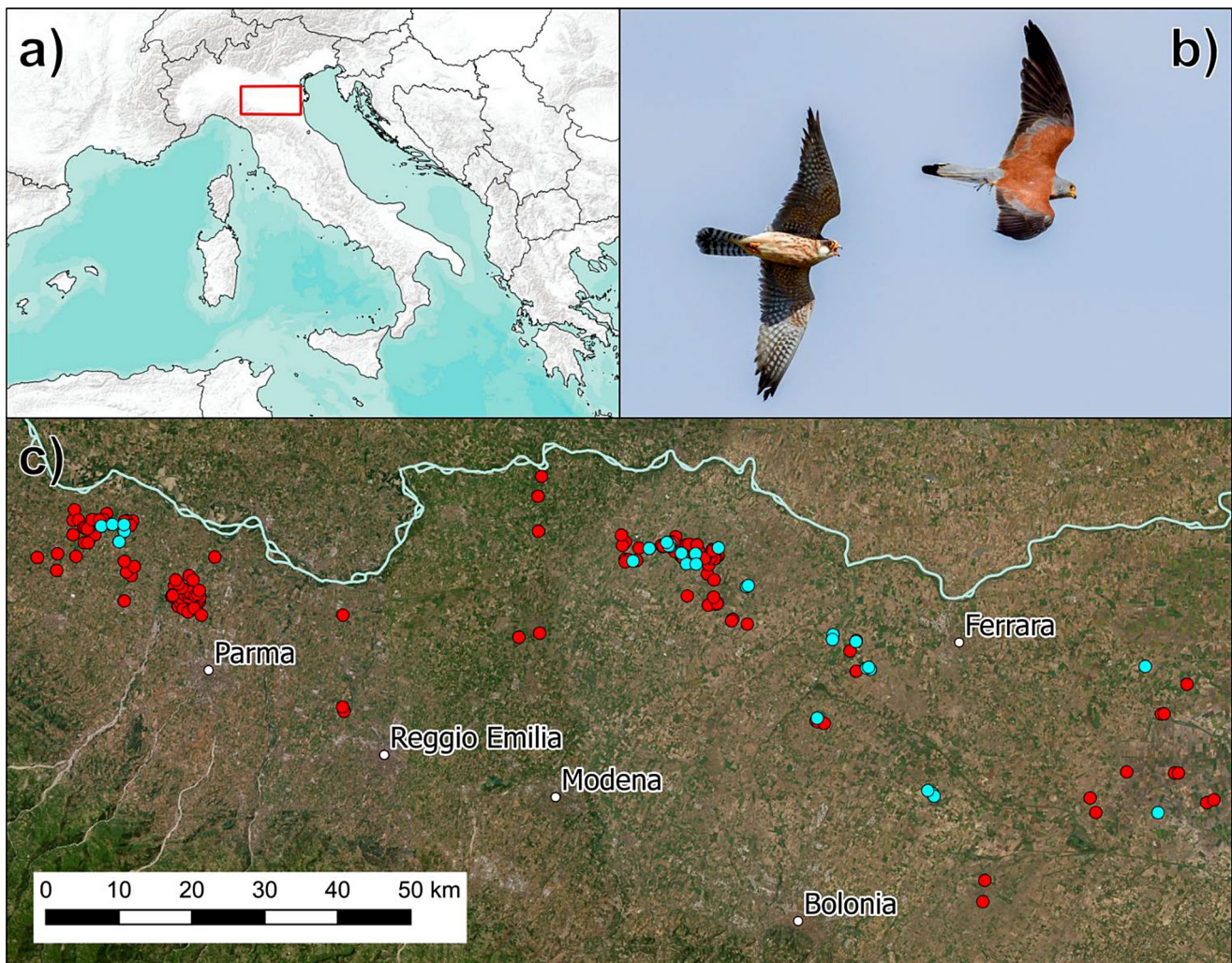


Fig. 1 a) Location of the study area (red square); b) red-footed falcon attacking a male lesser kestrel, in a typical kleptoparasitic attack (photo by F. Ambrosi); c) distribution of lesser kestrel colonies (blue

dots) and red-footed falcon nests (red dots) in the study area and period (2020–2022). The Po River (light blue line) and main cities are also highlighted

Foraging observations

To assess the frequency of kleptoparasitic behaviors, we focused our observations on foraging lesser kestrel groups, relying on the so-called scan sampling method (Altmann 1974). It was not possible to record data blind because our study involved focal animals in the field. Observations were carried out during three breeding seasons (April to July, 2020–2022). We conducted surveys from 50 vantage locations that provided excellent visibility near known lesser kestrel breeding sites, ensuring that no disturbance was caused by observers to foraging individuals located 50–500 m away. Observations were conducted between 06:00 am and 09:00 pm (GMT + 2) using binoculars (8–10×42) and spotting scopes (20–70×). An observation session started when we detected a group of two or more actively foraging lesser kestrels and lasted 15 min, during which we recorded the occurrence of red-footed falcons. If an interspecific interaction with a red-footed falcon took place, the session was prolonged for an additional 15 min, or until the interaction ended.

Characteristics of lesser kestrel foraging groups

During each session, we recorded the maximum number of foraging lesser kestrels (group size, hereafter). We associated each group of lesser kestrels with a specific colony by visually tracking the birds to observe which breeding site they returned to after each foraging event. Due to the open landscape of the study area, it was readily apparent to which colony the foraging individuals belonged. We measured lesser kestrels' foraging efficiency by calculating a "prey capture rate" expressed as the number of prey successfully captured during the observation session (visually estimated), corrected for groups size (number of prey/group size/min). Due to its key role in influencing the foraging probability of both species (Cioccarelli et al. 2022; AB, unpubl. data), we measured vegetation height (in cm) in the areas where lesser kestrels foraged by randomly taking measurements at five locations within a radius of 20 m from the foraging site. We recorded weather conditions during each observation session on a numerical scale with 1 representing full sun and 7 rainy weather (see Table S1). We categorized events involving chases between one or more red-footed falcons and a lesser kestrel from the foraging group as "attacks", while those without any such contacts were classified as "non-attacks".

Characteristics of interacting individuals

In 2021 and 2022, we gathered detailed characteristics of interacting individuals to identify factors influencing the

success or failure of red-footed falcon attacks. We evaluated the foraging tactics employed by lesser kestrels, distinguishing between two categories: (1) on-site foraging, when an individual consumes the prey for itself at the foraging site, or (2) colony foraging, when birds return directly to the colony after successful prey capture. Since multiple attacks (28%) were carried out by more than one red-footed falcons, we recorded the number of individuals involved in these attacks to evaluate their potential influence on the success of theft. We estimated prey size by comparing the length of the prey item relative to the claws of the lesser kestrel, following a method used in other studies (see Marchowski and Neubauer 2019; Busniuk et al. 2020). Prey were categorized by size: (1) "small prey" if they were smaller than the size of the claws, (2) "medium prey" with the same size as claws, and (3) "large prey" if larger than claws. The emission of alarm calls by lesser kestrels while being pursued by red-footed falcons was also recorded. We defined an attack as "successful" when the red-footed falcon successfully stole the food item from the lesser kestrel's claws or when the attacked lesser kestrel voluntarily dropped the prey. Conversely, an attack was categorized as "failed" if the lesser kestrel managed to escape with its prey.

Statistical analysis

To evaluate ecological factors associated with kleptoparasitic behavior, and the individuals' characteristics that determined the success or failure of the attacks, we relied on binomial generalized linear mixed models (GLMMs) fitted using the R package "glmmTMB" (Brooks et al. 2017) in R 4.0.3 (R Core Team 2022), with lesser kestrel colony identity ($N=22$) as a random intercept effect to account for non-independence of foraging groups belonging to the same colony.

We first fitted a binomial GLMM to investigate the ecological factors associated with kleptoparasitism attempts on foraging lesser kestrel groups as a response variable (non-attack=0; attack=1) and the following fixed effect predictors: group size, prey capture rate, vegetation height, weather conditions, time of day (hours after sunrise), day of the year (day 1 = January 1), and year (3-level factor). In a second binomial GLMM, we investigated the characteristics of interacting individuals in determining the probability of a successful attack (failed=0; successful=1), including the following fixed effect predictors: number of attackers involved, foraging tactic of lesser kestrel (2-level factor), emission of alarm calls (2-level factor), prey size (3-level factor), day of the year, and year (3-level factor). Quadratic effects of time of day and day of the year were tested in exploratory analysis but were invariably not significant and therefore were not included in models.

Model assumptions were checked by inspection of model outputs via the package “*performance*” (Lüdtke et al. 2021). Collinearity did not affect modelling ($VIF < 3$ in all models) (Zuur et al. 2010). Conditional and marginal R^2 were also computed using the package “*performance*”. Continuous predictors were mean-centred and scaled by their standard deviation to improve the interpretability and comparability of regression coefficients (Orlando et al. 2023). The significance of fixed effects was assessed by likelihood ratio tests. Means and variable estimates are reported together with their associated standard error unless stated otherwise.

Results

Frequency of kleptoparasitism

Kleptoparasitism by red-footed falcons on lesser kestrels was widespread across the study area and relatively frequent. Red-footed falcons were observed in 71.9% of lesser kestrel foraging group observation sessions ($N=332$ out of 462 sessions). We recorded attacks at 21 out of 25 lesser kestrel sampled colonies. Among sessions where the co-occurrence of the two species was detected, kleptoparasitic attacks took place in 45.8% of cases ($N=152$), typically as a single attack (but sometimes more), totaling 176 recorded attacks. Attacks were successful in 34.7% ($N=61$) of cases, with 28.4% ($N=50$) of attacks involving more than one red-footed falcon (2–4, mode: 2). Most of the observed

interactions (56.3%, $N=99$) involved only males of both species, while 18.2% ($N=32$) of attacks were performed by red-footed falcon males on lesser kestrel females, 15.3% ($N=27$) were by red-footed falcon females on lesser kestrel males, and 10.2% ($N=18$) involved females of both species.

Ecological and social factors affecting the frequency of kleptoparasitism and success of attacks

Prey capture rate significantly increased the probability that an attack by red-footed falcons took place (Table 1; Fig. 2). The probability of attacks markedly decreased in the course of the season (Table 1). Neither group size the environmental variables (vegetation height, weather, hour) had a statistically significant effect on the probability of attacks (Table 1). Kleptoparasitic attacks were significantly more frequent in 2020 than in 2021 and 2022 (Table 1).

The success rate of attacks was significantly lower when lesser kestrels rapidly moved away from the foraging site, whereas it significantly increased with the number of red-footed falcons engaging in the attack (Table 1; Fig. 2). In addition, it was significantly higher when lesser kestrels carried medium and large prey compared to small prey (Table 1; Fig. 2). The emission of alarm calls by lesser kestrel did not significantly affect the likelihood of a successful attack (Table 1).

Table 1 Binomial GLMMs exploring the ecological and social factors driving (a) the probability of red-footed falcon attack on a lesser kestrel foraging group and (b) the success rate of red-footed falcon -attacks on foraging lesser kestrels. Statistically significant predictors are highlighted in boldface. Marginal R^2 were calculated according to Nakagawa et al. (2017). Values in bold indicate statistically significant variables ($P < 0.05$)

Predictors	Estimate \pm SE	χ^2	df	P
a) Factors driving the probability of attack ($N=332$ sessions, marginal $R^2=0.24$)				
Number of lesser kestrels	0.06 \pm 0.09	2.02	1	0.16
Prey capture rate	7.68 \pm 3.53	18.14	1	< 0.001
Vegetation height	0.01 \pm 0.01	0.20	1	0.66
Weather	-0.23 \pm 0.97	0.22	1	0.64
Hour after sunrise	-0.01 \pm 0.05	0.15	1	0.70
Date (1 = 1st January)	0.18 \pm 0.15	12.24	1	< 0.001
Year^a	–	9.19	2	0.010
b) Factors determining the success of attacks ($N=176$ attacks, marginal $R^2=0.24$)				
Numbers of attackers	0.54 \pm 0.35	9.16	1	0.002
Foraging tactic (on-site vs. colony foraging)	0.76 \pm 0.35	4.01	1	0.045
Alarming	0.12 \pm 0.51	1.73	1	0.19
Prey size^b	–	14.80	2	< 0.001
Date (1 = 1 st January)	-0.05 \pm 0.90	0.08	1	0.78
Year (2022 vs. 2021)	0.03 \pm 0.72	0.01	1	0.93

^a: Estimated mean values (response scale): 2020 = 0.79^c \pm 0.08; 2021 = 0.51^d \pm 0.07; 2022 = 0.47^d \pm 0.07

^b: Estimated mean values (response scale): small = 0.17^e \pm 0.05; medium = 0.40^f \pm 0.07; large = 0.52^f \pm 0.08

Different superscript letters for estimated mean values indicate statistically significant differences ($P < 0.05$) in trait values between groups at *post hoc* tests

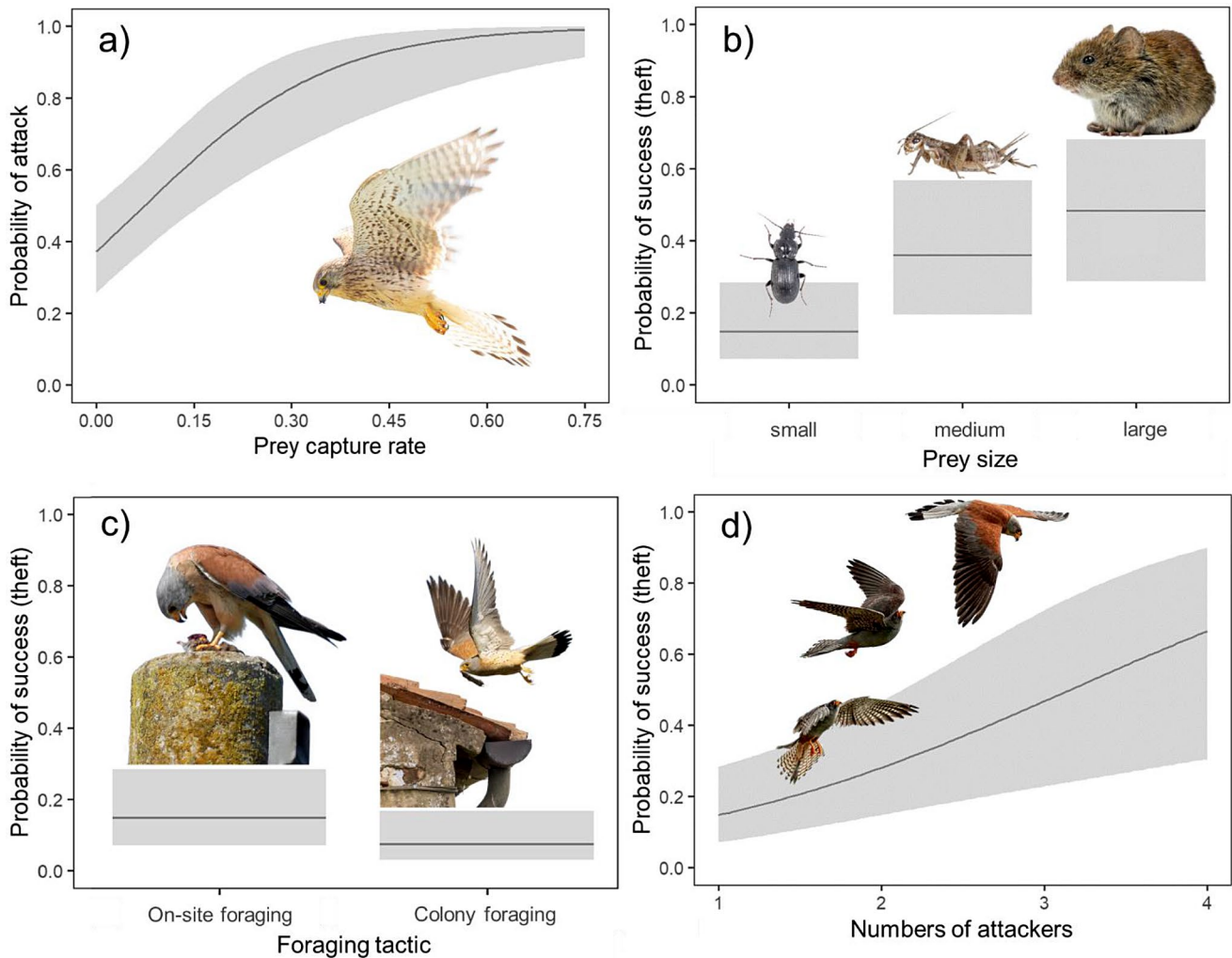


Fig. 2 Ecological and social factors significantly affecting frequency and success of kleptoparasitic attacks of red-footed falcons on lesser kestrels. **a)** The probability of occurrence of kleptoparasitic attack of red-footed falcon on lesser kestrel within mixed-species foraging groups increased with lesser kestrel foraging group prey capture

rate. Success rate of attacks was higher when **b)** lesser kestrels carried medium and large size prey; **c)** lesser kestrels foraged on-site; **d)** more than a single red-footed falcon was involved in the attack. Grey bands indicate 95% confidence interval

Discussion

To our knowledge, this study represents the first report of the systematic occurrence of kleptoparasitism among two falcon species. We argue that climate and land-use changes, that have recently led to the expansion of the breeding range of these two species, are the ultimate drivers of the emergence of this form of competitive interference. Large overlap of ecological niches between the two species, including foraging habitat selection and diet (AB, unpubl. data), and slight size asymmetries were likely the key elements favoring the emergence of kleptoparasitism.

Overall, our observations indicate that kleptoparasitism by red-footed falcons on lesser kestrels should not be viewed as an occasional or anecdotal behavior limited to a few individuals. Instead, it appears to be a specific foraging strategy occurring

in almost half of the cases when the two species were observed foraging together. It should be mentioned that our study did not involve individually marked birds, which makes it impossible to determine the true extent of this phenomenon; yet, the large number of observations broadly spread in time (from April to July, in 3 years) and space (~4,000 km², 22 different lesser kestrel colonies) suggest that the estimated frequency of kleptoparasitism across the study area is realistic.

Overall, food availability significantly influences ecological and evolutionary processes, including foraging (Bautista et al. 1998; Sherman and Eason 1998), often driving the emergence of kleptoparasitic behaviors (Herremans and Herremans-Tonnoeyr 1997; Senzaki et al. 2014). Our finding aligns with the expectations derived from optimal foraging theory (Pyke 1984): attacks were more likely when the foraging efficiency of lesser kestrel groups was higher and individual lesser kestrels

were more likely to suffer a prey theft when carrying medium-large prey. Hence, red-footed falcons displayed a remarkable foraging flexibility: they foraged independently but switched to kleptoparasitism when observing efficient foraging groups of lesser kestrels, minimizing risks associated with attacking similarly-sized (and potentially harmful) victims by pursuing them only when the food reward was greater. The latter result is consistent with observations from several kleptoparasitic systems (e.g. Ratcliffe et al. 1997; Spencer et al. 2017).

Lesser kestrels were better at escaping red-footed falcon attacks when flew directly to the colony after catching prey, probably carrying food for their nestlings or their partner. Flying away from the foraging area could be a strategy adopted by lesser kestrels to reduce vulnerability to attacks (Senzaki et al. 2014; Busniuk et al. 2020); unlike other kleptoparasitic species (e.g. gulls and skuas), red-footed falcons did not wait for victims near the breeding site. Instead, attacks typically occurred above cultivated fields during active foraging.

Moreover, our study revealed that kleptoparasitic attacks by multiple red-footed falcons had a higher success rate compared to attacks carried out by singletons. After the successful theft, agonistic behavior among aggressors was never observed. This might suggest that kleptoparasitic individuals may somehow cooperate to steal prey. While there are several previous records of cooperative hunting in birds (e.g. Ellis et al. 1993; Jarvey et al. 2022), cooperative kleptoparasitism is considered rare and mentioned mostly anecdotally (e.g. Yosef et al. 2012; Eakle et al. 2014; Camiña 2018). Kleptoparasitic attempts involved mostly two males, unlike cooperative hunting which is mostly performed by breeding pairs (Dekker 2009; Eakle et al. 2014; Camiña 2018; Leonardi 2020). Such a strategy may be promoted in order to receive the same support from conspecifics at the next possible opportunity and may also be promoted by the loose colonial breeding habit of red-footed falcons (Packer and Ruttan 1988).

Future studies should aim at investigating the impact of red-footed falcon kleptoparasitism on lesser kestrel fitness and its possible demographic consequences. Indeed, aggressive interference is expected to promote competitive exclusion (Amarasekare 2002). Asymmetries in aggressive interference may counteract asymmetries in resource exploitation and lead to the extinction of the least competitive and aggressive species (Grether et al. 2017). In the short term, red-footed falcon expansion might pose a challenge to local lesser kestrel populations, similar to what happened with the arrival of the black-winged kite (*Elanus caeruleus*) in Taiwan, where it reduced the abundance of the common kestrel (*Falco tinnunculus*) (Chen et al. 2022). Yet, in the medium-long term, kleptoparasitism can promote niche differentiation, leading to spatial or temporal segregation in resource use between the interacting species and lower

interspecific competition (Case and Gilpin 1974; Grether et al. 2009; Pfennig and Pfennig 2009), thus promoting coexistence (Carothers et al. 1984; Grether et al. 2017). More generally, our findings suggest that the reshuffling of biotic communities due to global changes may be accompanied by the establishment of novel forms of interactions, with potential implications at the population level.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03433-y>.

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Author contributions Conceptualization: AB, AM, DR, JGC, AM, MM Methodology: AB, AM, DR, JGC, DP, AM, MM Investigation: AB, DS, LE, GB, GA, NG, MM Visualization: AB, DS, LE, GB, GA, NG, MM Supervision: DR, AM, MM Writing: AB, DS, DR, AM, JGC, GB, GA, DP, AM, MM.

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Data availability The dataset supporting this article is available as Supplementary Material 2 (filename: ESM2_full_dataset_Berlusconi_kleptoparasitism_falcons.xlsx). Dataset is composed of three sheets: Groups, Individuals and Legend.

Declarations

Ethical approval Ethical approval was not needed for this study as no animals were subjected to manipulation during the research process. All activities complied with national laws.

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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