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Extreme number of second clutches in Common Kestrels *(Falco tinnunculus)* in Hungary

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Abstract Between 1995 and 2024, during a long term population monitoring of partially migratory Common Kestrels in Hungary, we identified potential second brooding pairs on several occasions. In 2020, we were able to conclusively prove the occurrence of second broods within the same breeding season. Following these findings, in 2023, during an exceptionally strong vole outbreak year, we identified the commencement of second broods in several waves. In 2023, a total of 379 Common Kestrel breeding attempts were observed, of which 42 involved second broods. While replacement broods were exclusively identified in closed kestrel-specific nesting boxes, second broods occurred both in artificial colonies and solitary sites, with breeding taking place in kestrel-designed nest boxes, as well as three cases in natural nests. In our study, we found that after a mild winter and a food-rich year, the earliest breeders were those that later attempted a second brood. Second-breeder Common Kestrels did not search for alternative nesting sites, and without exception, they reused the same nest used for their first brood. It is noteworthy that most second-brooding pairs started laying eggs for their second clutch before the young from the first clutch had actually fledged, meaning there was overlap between the two breeding attempts. On average, the initiation of the second clutch occurred two days earlier than the fledging of the last chick from the first clutch. Our observations suggest that Common Kestrels engage in second broods as an active strategy to enhance their reproductive success, rather than as a compensatory response to a low-success first clutch. We provide recommendations for adjustments in the monitoring of rodent-hunting raptor species that may exhibit similar adaptive responses.

Keywords: Common Kestrel, *Falco tinnunculus*, second broods, clutch initiation, clutch size, breeding success, Vásárhelyi-puszta, Hungary

Összefoglalás 1995 és 2024 között, parciálisan vonuló vörös vércséken Magyarországon végzett hosszútávú állomány-monitoring során több alkalommal is azonosítottunk lehetséges másodköltéseket. 2020-ban aztán egyértelműen sikerült bizonyítani másodköltés előfordulását ugyanazon költési időszakban. Ezt követően, 2023-ban, egy rendkívül erős mezei pocok gradációs évben, több hullámban azonosítottuk második költések megkezdését. 2023-ban összesen 379 vörös vércse költést figyeltünk meg, ebből 42 esetben másodköltésről volt szó. Míg pótköltéseket kizárólag zárt, vércséknek kialakított költőládákban azonosítottunk, a másodköltések mesterséges ládatelepeken és magányos pozíciójú költőládákban egyaránt előfordultak, sőt, három esetben természetes fészkekben is. Tanulmányunkban kifejtjük, hogy enyhe telet követő, táplálékban különösen gazdag évben azok a párok kezdték meg legkorábban a költést, amelyek később aztán másodköltéssel is próbálkoztak. A másodköltő vörös vércsék nem kerestek alternatív fészkelőhelyeket, és kivétel nélkül ugyanazt a fészket használták újra, amelyet az első fészekaljuk esetében választottak. Figyelemre méltó, hogy a másodköltő párok többsége még azelőtt megkezdte a második fészekalj lerakását, hogy az első fészekalj fiataljai ténylegesen elhagyták volna a fészket, azaz átfedés volt a két költés között. Átlagosan a második fészekalj tojásrakásának kezdete két nappal hamarabb következett be, mint hogy az első fészekalj legutolsó fiókája kirepült volna. Megfigyeléseink arra utalnak, hogy a vörös vércsék a másodköltést aktív stratégiaként alkalmazzák reproduktív sikerük növelésére, nem pedig kompenzáci-

ós válaszként egy alacsony sikerű első fészekaljra. Ajánlásokat adunk olyan rágcsálókat vadászó ragadozómadár fajok monitorozásának módosítására, amelyek hasonló adaptív válaszokat mutathatnak.

Kulcsszavak: vörös vércse, *Falco tinnunculus*, másodköltés, költéskezdés, fészekaljméret, költési siker, Vásárhelyi-puszta, Magyarország

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Introduction

Except tropical species, most diurnal birds of prey have only one brood per year (Newton 1977, 1979). However, in rodent-hunting raptors, some Nearctic species – such as the American Kestrel *(Falco sparverius)* (Stahlecker & Griese 1977, Toland 1985, Steenhof & Peterson 1997, Smith *et al.* 2017), the White-tailed Kite *(Elanus leucurus)*, the Black-shouldered Kite *(E. caeruleus)* (Pickwell 1930), and the Harris's Hawk *(Parabuteo unicinctus)* (Newton 1979) – have occasionally been observed to successfully raise a second brood. In South Africa, this phenomenon has also been identified in the Rock Kestrel *(F. rupicolus)* (van Heerden *et al.* 1994), which was previously considered a subspecies of the Common Kestrel *(F. tinnunculus)* until it was recently recognized as a separate species (Orta *et al.* 2020).

The timing of egg-laying in the Common Kestrel is highly variable and depends on weather conditions. Across the Western Palearctic breeding tends to start approximately six days later for every ten degrees of latitude northward (Carrillo & González-Dávila 2009). The egg-laying period can vary significantly across the species' range, but in Europe and Asia (north of the Himalayas), it generally occurs in April and May, with extremes recorded from March to July (Cavé 1968, Village 1990). This timing aligns with the classic spring and summer seasons of the temperate zone, though as shown, it can be prolonged and cover a wide time span.

Clutch size is one of the most important life-history traits in birds (Lack 1947, Stearns 1976, Price & Liou 1989), and successfully raising a second brood within the same breeding season not only demonstrates the parents' fitness and increases their reproductive success but also plays a crucial role in stabilizing a population and compensating for potential losses from previous years, affecting the recruitment numbers of individual birds (Newton 1979). However, such cases have been much less frequently documented in Palearctic raptor species.

The breeding success of the Common Kestrel has been widely studied across its range (e.g. Cavé 1968, Newton 1979, Cramp & Simmons 1980, Korpimäki 1984, Village 1990, Palokangas *et al.* 1992, Kostrzewa & Kostrzewa 1997). In this species, the first report of a second brood dates back to the mid-1980s (Závalský 1985). While Common Kestrels kept in captivity under controlled photoperiods have also been observed to produce a second clutch

(Meijer 1989, Meijer *et al.* 1992), only 17 field observations of a second brood following the successful rearing of the first have been reported in the species' breeding range until 2024, 14 cases from Europe (Závalský 1985, Glutz von Blotzheim *et al.* 1989, Sánchez 1990, Fargallo *et al.* 1996, Hudec & Šťastný 2005, Kotymán & Solt 2022) and three from Israel (Charter *et al.* 2005).

It appeared, therefore, that second broods in Common Kestrels were exceptional. While most documented cases describe isolated occurrences within a single season, field studies by Fargallo *et al.* (1996) found that three out of eleven Common Kestrel pairs initiated a possible second clutch. Similarly, a study in Israel reported second broods in Common Kestrel pairs nesting on buildings, with three cases documented in a single breeding season in 2004 (Charter *et al.* 2005).

A 2024 study from the Czech Republic revealed that in certain years with exceptionally high food availability, the occurrence of second broods is not as rare as previously thought (Poprach & Dusík 2024). The authors reported a total of 22 second broods over a long-term monitoring period from 1979 to 2019. The highest number, five second broods, was recorded in 2019, which was a year of Common Vole *(Microtus arvalis)* population gradation. However, unlike previous studies, the researchers also included replacement clutches following failed first broods in their count of second broods.

In Hungary, the Common Kestrel typically breeds once per year. Complete clutches laid as early as late March have been recorded, but it is also common for Common Kestrels to begin incubation only in mid-May (Haraszthy 2019, Kotymán & Solt 2022) which corresponds to the characteristics of the species, as reported in several studies, aligning with the identified dates of clutch initiation observed in multiple waves (Cavé 1968, Meijer 1989). The timing and dynamics of first clutches are influenced by external factors, as pairs frequently initiate replacement clutches if their original eggs are lost. In some cases, if the replacement clutch is also destroyed during the egg stage, they may even attempt a second replacement clutch (Haraszthy 2019, Kotymán & Solt 2022).

Haraszthy (2012) mentioned a full clutch found in an oological collection, where the first clutch of 5 eggs were collected on 25th April, and two new eggs were found in the same nest on 3rd May. This suggests that even an early May clutch could result from a replacement breeding attempt. At the other end of the breeding timeline, on 15th July 2004, two incubating pairs were observed between Karcag and Nádudvar in Hungary, while a third pair had not yet begun laying eggs (Bagyura *et al.* 2006).

We observed two cases of late broods in both 2001 and 2002, and one case in 2004 with nestlings that were most likely the result of second breeding attempts at the Vásárhelyi-puszta (Vásárhely Plain) (Bagyura *et al.* 2006). Subsequently, Kotymán and Solt in 2020 provided conclusive evidence of second broods in 2020 within a single breeding season (Kotymán & Solt 2022). We documented a Common Kestrel pair occupying a nest box, where the female began laying eggs on 20th March. Out of the clutch of six eggs five chicks fledged, remaining in the nest until late May or early June. Even after fledging, the young continued returning to the nest for several days, at which point a second clutch of three eggs had already appeared. The second clutch, initiated on 25th May and resulted in three nestlings (Kotymán & Solt 2022).

In the present study we describe documented cases of second-breeding attempts within the same breeding season in Common Kestrels in a sample area in southeastern Hungary, in 2023.

We describe also, how second broods were identified and investigate the weather/climate constraints hypothesis (Both & Visser 2001), whether pairs initiating a second brood tend to start their first breeding attempt earlier in year characterized by abundant food resources and favorable weather conditions. We also test the time-constraints hypothesis (Verhulst & Nilsson 2008), with particular attention to compensatory replacement clutches following offspring loss, as well as the timing and reproductive success of second broods. Furthermore, considering the environmental context, we investigate – within the framework of the reproductive output maximization hypothesis (Lack 1968, Newton 1979, Stearns 1992) – whether annual reproductive success can be effectively increased by second broods, and whether these additional breeding attempts serve a compensatory function or represent a true offspring-maximizing strategy.

Our aims also include to investigate:

1 – what the differences among pairs which engaged and did not engage in a second breeding attept are,
2 – how the onset and size of the first clutch influence the breeding success of the pairs with single and second broods,
3 – how population survey/monitoring work of this species needs to handle the occurence of second broods.

Materials and Methods

Study area

Our work is based on data collected during a long-term falcon monitoring program conducted between 1995 and 2024 in the Vásárhelyi-puszta, which is a typical Hungarian grassland, located in southeastern Hungary *(Figure 1)*. The Vásárhelyi-puszta spans approximately 8,000 hectares at the border of the Csongrádi-sík (Csongrád Plain) and the Békési-hát (Békés Ridge), within the administrative boundaries of Hódmezővásárhely, Békéssámson, Székkutas, Orosháza, and Kardoskút settlements (central co-ordinates): N 46˚28’25”, E 20˚37’30”). The central part of this area which covers 5,629 hectares, is designated as the core area of the Körös-Maros National Park. This perfectly flat landscape lies between 86–88.5 m a.s.l. Around 60% of the area is covered by short-grass steppe vegetation interspersed with agricultural fields (Kotymán *et al.* 2015).

The „Hódmezővásárhely környéki és csanádi-háti puszták” Natura 2000 site (HUKM10004 SPA) extends along the steppe, consists of large salt grasslands with marshlands surrounded by arable lands. We designated a 28,500-hectare study area in this region for long-term research. In this highly saline steppe landscape trees or small tree clusters have survived primarily at former homestead sites. Nest boxes were placed on these trees–partly in colonial, aggregated arrangements to support the settlement of Red-footed Falcons *(F. vespertinus)*,

and partly in scattered, solitary positions, most of which were occupied by Common Kestrels from the beginning of the monitoring program.

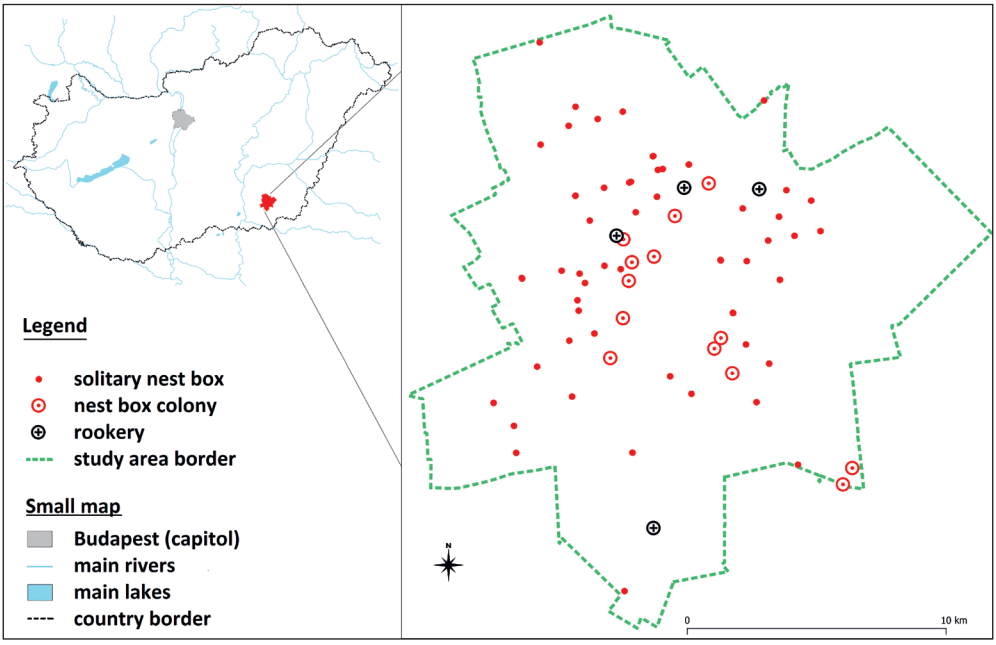

Figure 1. Spatial distribution of breeding sites (nestbox clusters, solitary nest boxes and rookeries) available long term at the Vásárhelyi-puszta Study Site, Hungary

1. ábra A Vásárhelyi-pusztán kialakított, hosszútávon elérhető fészekkínálat (költőláda-telepek, szoliter helyzetű odúk és vetésivarjú-telepek) térbeli elhelyezkedése

During the past 30 years we initially established four nest box clusters in the central part of the steppe, later increasing this number to 12 with 292 nest boxes in total in form of colonies containing 5–104 nest boxes, and in parrallel placed out 65 nest boxes also offering territorial nesting opportunities *(Figure 1)*.

Between 1995 and 2024, we examined 3,857 Common Kestrel breeding attempts, with the earliest recorded egg-laying occurring on 17th March and the latest on 25 July.

Data collection and selection

Regular data collection involved monitoring both nest boxes and naturally built nests suitable for falcons (such as those of Eurasian Magpie *(Pica pica)* and Hooded Crows *(Corvus cornix)*) within the colony sites. We also documented unusual nesting behavior, such as ground-nesting Common Kestrels (Kotymán 2005).

Throughout the 30-year period we conducted systematic inspections of nesting sites during all breeding season. We continuously checked every initial clutches, replacement clutches, and second broods, to determine whether a breeding pair had occupied a particular nest box (Kotymán *et al.* 2015). The frequency and criteria of these inspections were adjusted based

on the specific weather, temperature characteristics and food supply of each year. Monitoring periods began with the first visits between 15th and 25th March every year. Unoccupied nest boxes were checked up to five times per year until the end of July, while occupied boxes were monitored until the fledging or end of replacement and second breeding, typically until mid-August. Naturally occurring nests within the artificial colonies were monitored with the same frequency.

At each sampling site, we recorded the presence or absence of nesting, the species and the breeding status based on the stage of the reproduction. Between 1995 and 2009, the Rook *(C. frugilegus)* did not breed in the region, meaning that natural rook colonies were absent from the available nesting sites. The first rook colony was established within the study area in 2009, allowing us to begin regular surveys of falcons nesting in these newly formed colonies in addition to our previous monitoring efforts. This is important and interesting because, under natural conditions, this nest-building species serves as one of the main "nest sources" for small falcons, which do not build nests of their own.

Between 2020 and 2023, beyond the regular monitoring of the artificial nest box network and rook colonies, we conducted a full census to assess the entire Common Kestrel and Red-footed Falcon population across the 28,500-hectare study area. This census documented all recorded breeding attempts, including those in typical falcon nesting sites such as Magpie and Hooded Crow nests, as well as in various atypical locations. These included natural tree cavities, crevices in broken tree trunks, abandoned farmsteads, buildings, ruins, ledges, and even ground nests (Solt *et al.* 2024).

Between 1995 and 2019, repeated observations documented cases in which the same pair of Common Kestrels initiated a second clutch while their first brood was still in the nest and the nestlings were nearing fledging. Although individual marking of the species was not conducted during this period, it was clear that the same female (pair) was involved. This was evident from their aggressive behavior towards other females, which is consistent with our previous observations and also with existing knowledge that female Common Kestrels are aggressive towards intruding females during the breeding season (Wiklund & Village 1992). This makes it unlikely that a different female could successfully lay eggs in an occupied nest.

Breeding pairs consistently displayed strong defensive behavior against intruding females and fledglings from other nests, actively chasing them away. In contrast, they tolerated their own fledged young from the previous clutch, which were even observed begging for food from the female incubating the second clutch. Despite this additional demand, neither parent displayed aggression towards their earlier offspring.

In 2023 we not only systematically tracked apparent cases through regular monitoring of breeding pairs, and direct observations, but we also used individual color-ring marking regularly.

We categorized nesting events, particularly in relation to bird reproduction.

Replacement clutches: These are new clutches laid after the failure of the first clutch during one of the key stages = egg-laying, incubation, or chick-rearing. The failure of the first clutch prompts the bird to lay a second clutch, hence the term „replacement."

Unsuccessful nestings: These are situations where a nesting attempt is made (i.e. a clutch is initiated), but it ultimately does not lead to fledging, meaning any predation and egg-losses, or when the chicks do not survive or are not able to leave the nest. In the case of 5 singlebrood and one secondbrood nests the detection of breeding success failed and data of these nests was excluded during comparison successful and unsuccessful nests.

We identified **second broods** only in cases where the pair's first breeding attempt was proven successful–that is, they had successfully reared at least one chick. Additionally, second broods were confirmed through individual markings or the pair's distinct behavior, particularly their tolerance towards the fledglings from the first brood and the presence of both parents roosting together. The juveniles from the first brood often spent most of the day with the incubating female of the second clutch. Replacement clutches following failed breeding attempts were explicitly excluded, even if failure occurred during the chick-rearing stage.

Based on our observations, we determined that fledglings remained near the nest for at least 15 days after their first documented departure. We recorded the start dates of breeding attempts, the appearance of the first eggs in replacement clutches, and the initiation of second broods. Additionally, we calculated the interval between the actual fledging of the first brood and the start of replacement or second clutches, using Julian days (where day 1 = January 1). Nestlings were marked with standard ornithological rings and color rings between 19 and 27 days of age.

For group formation and comparison, we selected broods considered to be definitively single-brood based on the initiation date of the first occurrence of replacement broods. The resulting subset of single broods, the replacement broods, and the second broods were defined as the categories for comparison. In this analysis, only single broods that commenced prior to the appearance of replacement broods were included.

For second broods, separate groups were established according to the outcome of the second attempt, enabling the assessment of parameters associated with both successful and unsuccessful breeding attempts.

All statistical analyses were performed in R version 4.0.5 (R Core Development Team 2021). The studied variables of the investigated groups had non-normal distribution detected by Shapiro–Wilk test. We used non-parametric tests for the comparison of the investigated groups (Wilcoxon signed-rank test for pairwise comparison, Kruskal–Wallis test for multiple comparison with application of Dunn Test for pairwise comparison of groups by Holm method, considering two-sided tests) and for investigation of correlations between studied variables (Spearman's rank correlation).

Results

In 2023 – in a year of strong Common Vole population growth and with an abundance of insect prey – we identified multiple waves of second breeding attempts.

Out of a total of 325 occupied nest with attempted Common Kestrel breeding, according to the stringently formulated conditions, 271 were classified as single broods, 12 cases were

Table 1. Initiation day of first clutch of the three groups
1. táblázat Az első, pót- és másodköltések kezdő napja a három csoportban

Type of broods	Mean (SD)	Min	Median	Max	n
Single broods	122.37 (19.57)	78	122.0	206	271
Replacement clutches	113.33 (13.19)	93	112.5	136	12
Second broods	90.05 (10.96)	76	87.5	119	42

classified as replacement broods, and 42 as confirmed having second broods *(Table 1)*. We categorized the clutches into three groups: those that only were single breeding attempts, those where a replacement clutch occured following a failed first attempt, and those where successfully fledged young from the first clutch and subsequently the pair initiated a second brood. Second clutches occurred in both artificial colonies and solitary nesting sites (in both nest boxes and natural nests). Most of these occurred in kestrel nest boxes, only three cases were observed in natural nests. Replacement clutches were exclusively found in closed nest boxes specifically designed for Small Falcons *(Figure 2)*.

We considered only those single broods during our further comparison where nesting was initiated before Julian day 120 to exclude potential replacement clutches. This date is based on the earliest day of first initiation of documented second breeding attempts (Julian day119). Because of this criterion it was only possible to use 126 single broods out of the total of 271 for the further comparison of pairs with single or second broods *(Table 2)*.

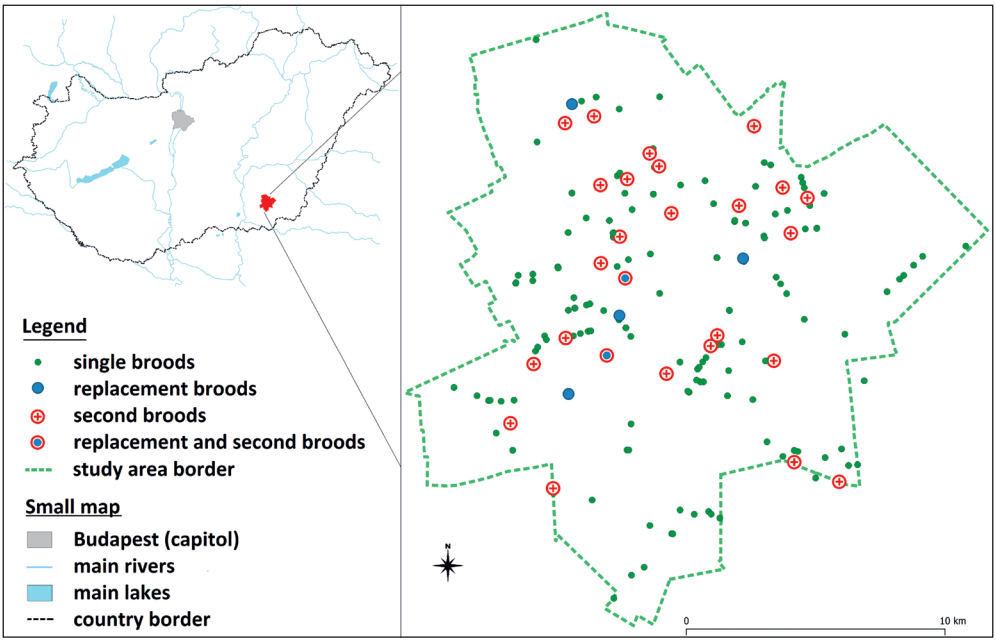

Figure 2. Spatial distribution of single, replacement and second broods in 2023 at the Vásárhelyi-puszta study site, Hungary
2. ábra Az első, pót- és másodköltések térbeli eloszlása 2023-ban a Vásárhelyi-puszta mintaterületen

The proportion of second broods among all successful nests where at least one nestling fledged in the first clutch was 16,6% in 2023 in the studied population. Second broods are not restricted to Rook colonies, artificial nest-site clusters or colonies in general; rather, they are distributed much more evenly across the landscape.

Initiation date and size of the first clutch of the single, replacement and second broods

The initiation date of the first clutch differed significantly among the three groups ($\chi^2_{,2}$=53.137, p < 0.001, Kruskal–Wallis test) *(Figure 3)*. Pairwise comparison of these three groups shows also strongly significant difference in the initiation day of the first clutch between pairs with a single brood or second brood and between pairs with a replacement brood or second brood also (p < 0.001), but no significant difference was found between pairs with single and replacement broods (p = 0.264). Pairs having second broods started their first clutch the earliest (p < 0.001, Kruskal–Wallis multiple comparison) *(Table 2)*.

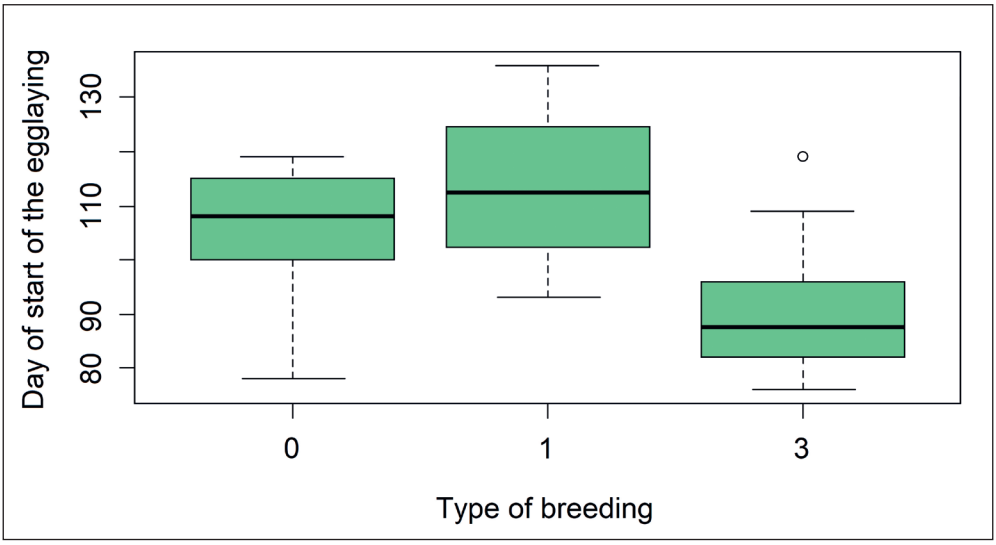

Figure 3. The breeding initiation dates of the first clutch among the pairs with singlebrood nests (0), replacement brood (1), and second broods (3)

3. ábra Az egy költéses fészkek (0), a pótköltések (1) és a másodköltő (3) párok első fészekalja költéskezdés szerint

The number of eggs in the first clutch differed significantly among the three groups ($\chi^2_{,2}$=18.108, p < 0.001, Kruskal–Wallis test) *(Table 2)*. Pairwise comparison of the three groups shows strong significant difference in the number of eggs in the first clutch between pairs with a single brood or a replacement clutch (p = 0.02) between pairs with a single brood or second brood (p = 0.002), and the difference was not significant between groups with replacement and second brood. Pairs having a single brood had the largest number of eggs in their first clutch (p = 0.02, Kruskal–Wallis multiple comparison) *(Figure 4)*.

Table 2. Initiation and clutch size of the first clutch of the three groups
2. táblázat Az első, pót- és másodköltések kezdő napja és fészekaljmérete a három csoportban

Type of broods	Breeding initiation days (Julian day)				Clutch size (# of eggs layed)				n
	Mean (SD)	Min	Median	Max	Mean (SD)	Min	Median	Max	
Single broods	106.56(9.74)	78	108.0	119	5.18(1.16)	1	5.0	8	126
Replacement clutches	113.33(13.19)	93	112.5	136	3.92(1.73)	1	5.0	6	12
Second broods	90.05(10.96)	76	87.5	119	4.55(1.09)	2	5.0	7	42

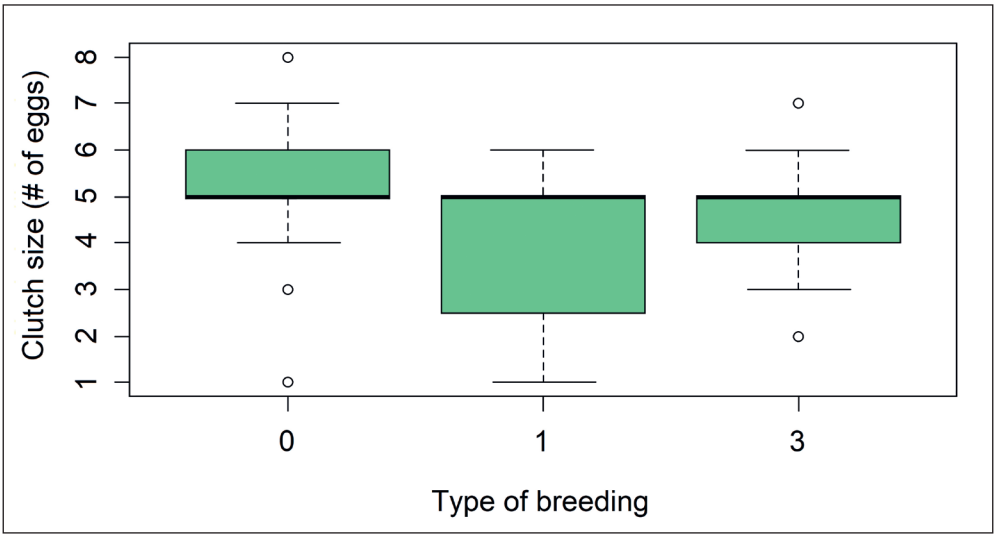

Figure 4. The number of eggs in the first clutch of the pairs with single-brood nests (0), replacement-broods (1), and second broods (3)
4. ábra Az egy költéses párok (0), a pótköltések (1) és a másodköltő (3) párok első fészekaljmérete (tojások száma)

Single clutches

Comparing successful and unsuccessful pairs with single brood, we found that the successful pairs initiated their clutch significantly earlier ($W = 1383.5$, $p < 0.01$, Wilcoxon rank test) *(Figure 5, Table 3)*.

The number of eggs did not differ between successful and unsuccessful pairs with a single brood ($W = 654.5$, $p = 0.39$, Wilcoxon rank test) *(Table 3)*.

Second broods

We did not find significant differences in the initiation day of the first clutch between pairs with successful and unsuccessful second brood ($W = 232$, $p = 0.323$, Wilcoxon rank test), but both the mean and median values of the date show an earlier start of egg laying in successful cases *(Figure 6, Table 4)*.

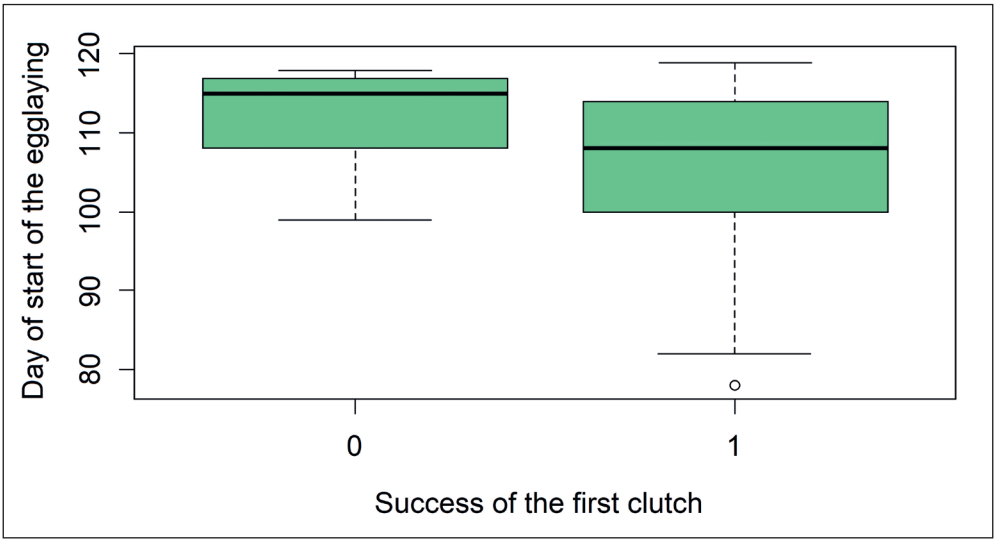

Figure 5. Comparison of the initiation of the clutch of unsuccessful (0) and successful (1) pairs having only a single brood

5. ábra A tojásrakás kezdetének összehasonlítása a sikertelen (0) és sikeres (1) párok között, amelyek csak egyetlen költést neveltek

Table 3. Initiation dates and clutch sizes of unsuccessful and successful single broods

3. táblázat A sikertelen és sikeres egyetlen költések kezdő napja és fészekaljmérete

Type of broods	Breeding initiation days (Julian day)				Clutch size (# of eggs layed)				n
	Mean (SD)	Min	Median	Max	Mean (SD)	Min	Median	Max	
Unsuccessful	112.50(5.57)	99	115.0	118	4.94(1.30)	1	5.0	6	20
Successful	106.02(9.81)	78	108.0	119	5.25(1.14)	1	5.0	8	101

Table 4. Parameters of the start of the two breeding attempts of unsussessful and successful double breeders

4. táblázat A második költés terén sikertelen és sikeres másodköltéses párok első és második költéskezdésének adatai

Type of brood	First breeding initiation days (J. d.)				Second breeding initiation days (J. d.)				n
	Mean (SD)	Min	Median	Max	Mean (SD)	Min	Median	Max	
Unsuccessful	92.53(11.64)	76	90.0	119	171.87(16.05)	139	174.0	195	15
Successful	89.15(10.43)	76	86.0	119	163.23(8.54)	149	162.0	179	26

There were near significant differences in the initiation day of the second clutch between pairs with successful and unsuccessful second broods (W = 264, p = 0.063, Wilcoxon rank test) *(Table 4)*, the pairs with a successful second brood started the egglaying of the second clutch earlier *(Figure 7)*.

There was no significant difference in the number of eggs in the first clutch between pairs with successful and unsuccessful second broods (W = 178, p = 0.634, Wilcoxon rank test) *(Table 5)*.

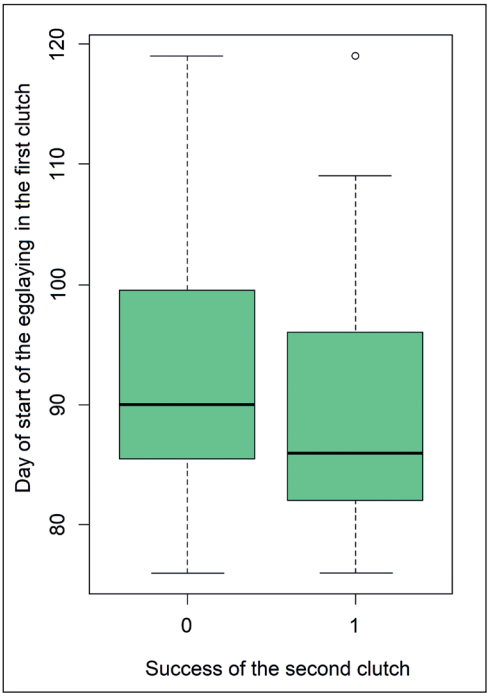

Figure 6. Comparison of unsuccessful (0) and successful (1) double breeders by day of the start of egglaying for their first clutch

6. ábra Második költésük terén sikertelen (0) és sikeres (1) másodköltők első költéskezdésének alakulása

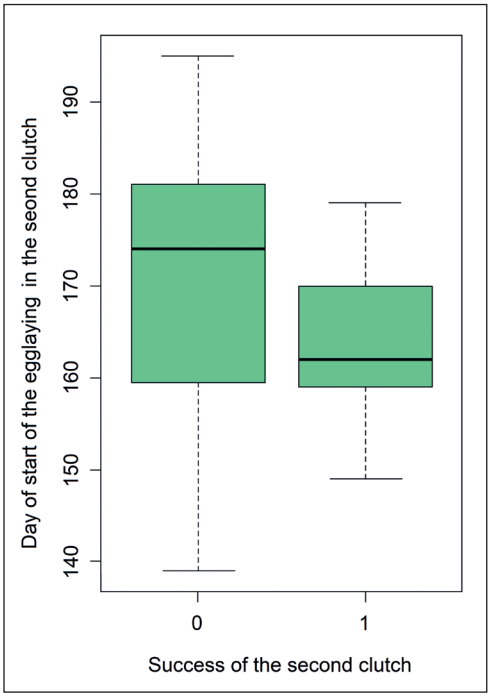

Figure 7. Comparison of unsuccessful (0) and successful (1) double breeders by the starting day of egglaying in their second clutch

7. ábra Második költésük terén sikertelen (0) és sikeres (1) másodköltők második költéskezdésének alakulása

Table 5. Clutch size of unsuccessful and successful double breeders in their two breeding attempts based on and categorized by their success in the second breeding attempt

5. táblázat A sikertelen és sikeres másodköltéses párok első és második költésének fészekaljmérete, a második költés kimenetele szerinti sikertelen és sikeres csoportok szerint

Type of broods	Clutch size of First breeding attempt				Clutch size of Second breeding attempt				n
	Mean (SD)	Min	Median	Max	Mean (SD)	Min	Median	Max	
Unsuccessful	4.53(1.19)	2	5.0	7	2.73(1.53)	1	2.0	5	15
Successful	4.65(0.94)	2	5.0	6	4.08(0.69)	3	4.0	5	26

The initiation of second clutches occurred, on average, 76 days after the start of the first clutch (mean = 75.67 days, SD = 10.39 days, median = 76 days, n = 42). The initiation of the first clutch shows a significant correlation with the initiation of the second clutch in pairs with second broods ($r = 0.688$, $p < 0.001$, Spearman's rank correlation).

Regarding unsuccessful and successful second clutches, no significant difference was found in the elapsed days between the initiation date of the first and second clutches (W =

Table 6. The time interval between the initiation of the two clutches in second breeders within the groups of unsuccessful and successful second-brooding pairs

6. táblázat A másodköltők két költéskezdése között eltelt időablak a második költés terén sikertelen és sikeres másodköltésű párok csoportjában

Type of second brood	Days elapsed between the start of the two broods				n
	Mean (SD)	Min	Median	Max	
Unsuccessful	79.33 (12.98)	59	79.0	105	15
Successful	74.08 (8.02)	51	76.0	87	26

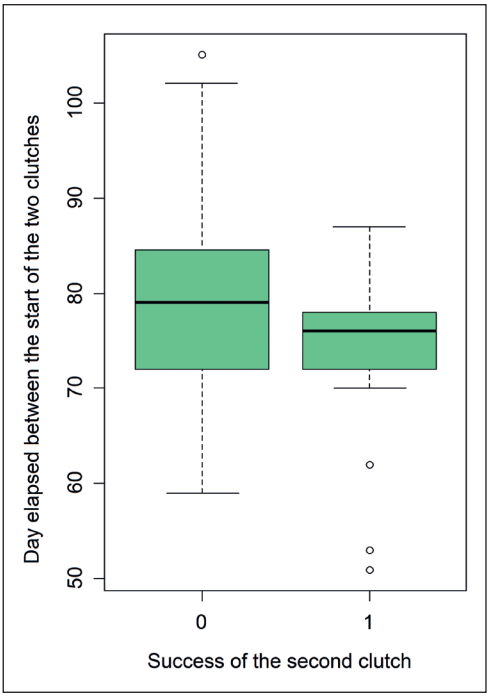

Figure 8. Comparison of time elapsed between the two clutch initiations of unsuccessful (0) and successful (1) second-brooding pairs

8. ábra Második költés terén sikertelen (0) és sikeres (1) másodköltésű párok két költéskezdése között eltelt idő alakulása

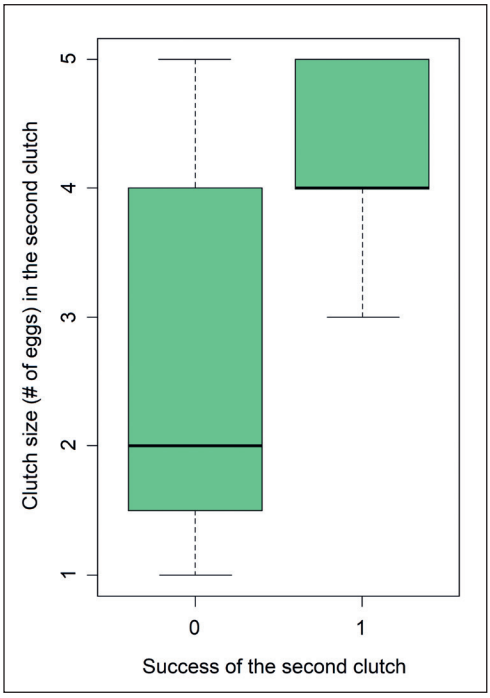

Figure 9. Comparison of unsuccessful (0) and successful (1) double breeders by the number of eggs in their second clutch

9. ábra Sikertelen (0) és sikeres (1) másodköltők második költésének fészekaljmérete

246.5, p = 0.167, Wilcoxon rank test) *(Table 6)*, but this interval is probably shorter in pairs with a successful second brood *(Figure 8)*.

There was a temporal overlap between the first and second breeding attempts. Based on the assumption that the first brood remains near the nest for 15 days after fledging, the overlap period was approximately 2 days (mean = -1.62 days, median = -2 days, SD = 9.80 days).

Table 7. Total number of fledged nestlings of single and double breeders
7. táblázat Az egy költéses és másodköltéses párok együttes kirepített fiókaszáma

Type of broods	Total fledging numbers				n
	Mean (SD)	Min	Median	Max	
Single broods	3.744 (2.068)	0	4.0	6.00	121
Double broods	6.293 (2.472)	1	6.0	10.00	41

There was a significant difference in the number of eggs in the second clutch between pairs with successful and unsuccessful second broods ($W = 96.5$, $p < 0.01$, Wilcoxon rank test), successful double breeders had larger second clutches *(Figure 9)*.

Comparison of the total number of fledged nestlings between pairs with a single brood and second brood showed that pairs with second broods had significantly more fledged nestlings ($W = 1225.5$, $p < 0.001$, Wilcoxon rank test) *(Table 7)*.

Discussion

Identification of second clutches

Observations confirmed that, similar to findings in American Kestrels (Toland 1984), Common Kestrel pairs raising their first clutch also actively defended their nesting site from intruders – including neighboring pairs in aggregated colonies, other raptors, corvids, mammalian predators, and even humans – while remaining tolerant towards their own first brood, even when fledglings stayed to linger near the nest:

- The male continued to provide food, which the female distributed while incubating the second clutch (as also documented by Toland 1985).
- Egg-laying for the second clutch began even before the fledglings from the first clutch had completely left the nesting site, suggesting that the parents initiated their second breeding attempt while still caring for their first-fledged young.
- First brood fledglings frequently remained near the nest, initially maintaining close contact with the female incubating the second clutch, sometimes even surrounding her while she incubated the new eggs from the second brood.
- After fledging, the first-brood juveniles continued to return to the nest for at least two weeks, in some cases up to three weeks to roost.

As also observed in American Kestrels (Toland 1985), pairs that produced two clutches initiated their first clutch the earliest. Interestingly, and importantly, not only the earliest breeders produced a second clutch.

The pattern of earlier breeding being associated with larger clutch sizes has been observed in several falcon species including American Kestrels (Toland 1985), in captivity (Bird & Lague 1982), and also in field studies of Common Kestrels (e.g. Cade 1982). Similarly, in captivity, it has been shown that earlier breeders tend to have larger clutches, and as the season progresses, clutch size declines (Meijer 1989). In line with this, as seen in American

Kestrels – and many other temperate-zone bird species – earlier breeders tend to produce more offsprings (Steenhof & Heath 2013) and have higher return rates (Steenhof & Heath 2009) than later breeders.

Generalist predators may advance their nesting period in response to prey availability changes. Such shifts may eliminate earlier constraints that would otherwise hinder early breeding, such as seasonal declines in reproductive success (Gienapp & Visser 2006) or competition for higher-quality mates (Smith *et al.* 2017).

For the Common Kestrel, the main prey is the Common Vole. The population dynamics of this small mammal show multi-annual fluctuations (Tkadlec & Stenseth 2001) and can produce mass outbreaks (Jacob *et al.* 2014), such as the one that occurred in 2023. In our study of partially migratory Common Kestrels in the Pannonian Basin we observed that after a mild winter with abundant food, the earliest breeders were typically those that later attempted a second clutch. However, single-brooded pairs had the largest clutch sizes, and among them, the successful pairs started breeding significantly earlier. Yet, there was no difference in the clutch sizes of successful and unsuccessful single-brooded nests. Common Kestrels are small-mammal specialists that respond to fluctuations in prey abundance through several adaptive mechanisms, such as adjusting their clutch size and immigrating to areas with high prey density (Korpimäki & Norrdahl 1991). It appears that, for this species, recent changes in weather (warming, mild winter, drier summers) in the region, together with abundant food availability in a given year, have also allowed for second broods as an adaptive response.

Returning again to the American Kestrel as a parallel, it remains to be seen whether these trends will continue, and how early breeding – and particularly the higher total number of offsprings in double-brooded pairs – will affect the American Kestrel's survival (Smith *et al.* 2017).

An interesting finding of our study, in contrast with results from American Kestrels (Toland 1985), or Common Kestrels studied by Fargallo *et al.* (1996) and Charter *et al.* (2005), is that the second-brooding Common Kestrels we studied did not search for alternative nesting sites. They reused the same nest which they used for their first clutch without exception.

A possible explanation for the above is provided by the census conducted in the study area between 2020 and 2023, which indicates that the availability of nesting sites for kestrels is approaching saturation. In other words, aside from the nest boxes, virtually no vacant natural nests were available for breeding Common Kestrels in 2023.

It is also noteworthy that out of 42 pairs, 29 (69%) began laying eggs for their second clutch before the young from their first clutch had fledged – meaning there was an overlap between the two breeding events. In some cases, the theoretical date of nest departure for the first brood coincided with the start of the second clutch, as observed in American Kestrels by Porter and Wiemeyer (1972), who found in captive birds that the second clutch was sometimes laid before the young from the first had fledged.

In our study, the average interval between the fledging of the last chick and the beginning of egglaying for the second clutch was -2 days (range: -25 to +27 days).

Strategy or compensation?

While second breeding attempts are well-documented in species like the Common Barn Owl *(Tyto alba)* (e.g. Poprach *et al.* 2010, Béziers & Roulin 2016, Bank *et al.* 2019), this is not the case in Common Kestrel. It is possible that Common Kestrels exhibit this behavior more frequently than previously assumed, especially in certain years with favorable conditions (e.g. high prey availability). However, in contrast to what Béziers and Roulin (2016) observed in Common Barn Owl –where second broods serve to compensate for failed first broods – which were in terms of our explanations recruitment broods – and low first-breeding success – our observations suggest that Common Kestrels engage in second broods as an active strategy to enhance overall reproductive success, rather than as a compensatory response to a failed or low-success first clutch.

Pairs that produced second broods started breeding the earliest. Both among pairs with single and both second broods, the early breeders had higher chance for successful breeding, which can indicate the high quality of these pairs. Among early breeders, the pairs with second broods had lower clutch size in their first clutch than the pairs with a single brood, which may raise that pairs with second broods „prepared" themselves for a second clutch. The larger size of successful second clutches indicates the high quality of these pairs and their strategy to maximalize reproductive success in the case of extremely good food availability, while results indicate that single-brooded and second-brooding pairs do not differ in the size of their first clutch *(Table 2, Figure 4)*. In contrast, the total annual number of fledglings shows a significant difference.

A key factor behind the above explained may be that generalist species, or those foraging in heterogeneous habitats, are likely less sensitive to mismatches between food availability and the timing of food peaks compared to specialist species (Visser & Both 2005). It is likely that food abundance, favorable prey accessibility, and optimal weather conditions together determine whether Common Kestrels can begin breeding early enough to raise two broods in a single season (Newton 1979). Warm, dry spring weather improves hunting success and enhances the female's physical condition (fat and protein reserves), which are critical for egg development (Cavé 1968). In contrast, cold, wet spring weather increases energy demands, reduces hunting success, and thereby decreases the likelihood of successful reproduction (Cavé 1968). Early-breeding Common Kestrels face a dilemma if conditions are or become unfavorable, weather may be fickle in the early spring period, the risk of clutch failure increases, but under optimal conditions, early breeding provides enough time to attempt a second, successful brood (Toland 1985).

Implications for monitoring programs

In traditional monitoring programs follow-up observations after fledging are often limited due to logistical constraints or other scheduled research activities. This can result in missing the detection of second clutches, unless the second egg-laying overlaps with the presence of first-brood juveniles–a scenario that naturally draws attention to the phenomenon.

Suggested Adjustments to monitoring protocols

To improve detection of second broods, at least one follow-up inspection should be conducted 10 to 25 days after the documented fledging event.

This additional monitoring could help identify overlaps between first and second broods, ensuring a more accurate understanding of breeding patterns.

Possibility of similar patterns in other rodent-hunting raptors

Considering the observed relationship between second broods and high prey availability (e.g., vole outbreaks), it would be worth investigating other rodent-hunting raptor species that may exhibit similar adaptive responses.

Climate change and ecological shifts may further influence prey population cycles, leading to unexpected breeding adaptations in various predator species. An important consideration is that all published data cited on second broods originate from regions characterized by long vegetation periods, where Common Kestrel populations are either non-migratory or only partially migratory. In other words, these data do not come from the Alps or Scandinavia, where Common Kestrels have a much shorter breeding window. Nevertheless, climate change is likely to expand the geographical areas suitable for second brooding. It is also important to acknowledge that, conversely, portions of the breeding range may experience habitat degradation, potentially resulting in semi-arid conditions that would no longer support second broods.

Future research should assess whether other rodent-dependent raptors (e.g. owls, harriers and small falcons) exhibit similar multi-brood reproductive strategies in response to rodent population peaksand optimal weather conditions.

By refining monitoring efforts and expanding the focus to include other raptor species, we may uncover previously undocumented reproductive behaviors driven by environmental variability and fluctuations.

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