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Use of Monk Parakeet Nests by American Kestrels in Central Argentina

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ABSTRACT.—American Kestrels (*Falco sparverius*) are cavity adopters, meaning they depend on pre-existing cavities for nesting. We investigated the use of natural cavities by kestrels during three consecutive breeding seasons in the *caldén* (*Neltuma caldenia*) forests of central Argentina. We recorded 74 nesting attempts in 49 unique cavities. These attempts were distributed among Monk Parakeet (*Myiopsitta monachus*) nests (74.3%), excavated cavities (10.8%), non-excavated cavities (9.5%), and Brown Cacholote (*Pseudoseisura lophotes*) nests (5.4%). Monk Parakeet nests were frequently reused (93.8%) in subsequent seasons. In 87% ($n = 13$) of the reused nests, Monk Parakeets were also occupying other nest chambers. Physical cavity characteristics, such as height, depth, cardinal orientation, inclination and entrance area, were unrelated to cavity reuse. However, Monk Parakeet nests appeared to play an important role in kestrel nesting strategies. Our findings suggest that Monk Parakeets act as ecosystem engineers, facilitating kestrel nesting opportunities in the *caldén* forest. Further research is needed to understand whether these interactions provide similar benefits in other landscapes where Monk Parakeets have expanded their range.

KEY WORDS: *breeding*; *cavity adopter*; *ecosystem engineer*; *nest*; *reproduction*; *sympatric interaction*.

USO DE NIDOS DE *MYIOPSITTA MONACHUS* POR *FALCO SPARVERIUS EN EL CENTRO DE* ARGENTINA

RESUMEN.—*Falco sparverius* es una especie que adopta cavidades y depende de éstas para anidar. Investigamos el uso de cavidades naturales por parte de *F. sparverius* durante tres temporadas reproductivas consecutivas en los bosques de *Neltuma caldenia* del centro de Argentina. Registramos 74 intentos de anidación en 49 cavidades únicas. Estos intentos se distribuyeron entre nidos de *Myiopsitta monachus* (74.3%), cavidades excavadas (10.8%), cavidades no excavadas (9,5%) y nidos de *Pseudoseisura lophotes* (5.4%). Los nidos de *M. monachus* fueron las cavidades más frecuentemente reutilizadas durante las temporadas (93.8%). En el 87% de los nidos reutilizados ($n = 13$) también había individuos de *M. monachus* haciendo uso de otras cámaras del nido. Las características físicas de las cavidades, como altura, profundidad, orientación cardinal, inclinación y área de entrada, no mostraron relaciones significativas con la reutilización de cavidades. Sin embargo, los nidos de *M. monachus* parecen desempeñar un papel importante en las estrategias de nidificación de *F. sparverius*. Nuestros hallazgos sugieren que *M. monachus* actúa como ingeniero del ecosistema, facilitando oportunidades de nidificación para *F. sparverius* en el bosque de caldén. Se necesitan más investigaciones para comprender si estas interacciones proporcionan beneficios similares en otros paisajes donde *M. monachus* ha expandido su área de distribución.

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INTRODUCTION

The American Kestrel (*Falco sparverius*) is a cavity-adopting species as it requires pre-existing cavities for nesting (Smallwood and Bird 2020). This species inhabits a wide range of environments across the Americas and typically nests in tree cavities excavated by woodpeckers or non-excavated cavities formed by natural processes such as decay. Although much of what is known about kestrel breeding biology comes from studies using artificial nest boxes, there is limited information on the species use of natural cavities in wild habitats.

In addition to tree cavities, kestrels also breed in nests of other bird species, such as the Brown Cacholote (*Pseudoseisura lophotes*) and Monk Parakeet (*Myiopsitta monachus*; Martella et al. 1985, de La Peña 2013, Tracey and Miller 2018). Monk Parakeets nest colonially, and act as ecosystem engineers, building large communal stick nests with multiple irregular internal chambers that provide valuable nesting opportunities for kestrels and other cavity-adopting species (de Lucca 1992, Eberhard 1998, Diamond 2017, Burgio et al. 2020, Battisti and Fanelli 2021). The use of Monk Parakeet nests by a variety of cavity users highlights the ecological role they play in supporting other species (Salvador 2014).

The expansion of Monk Parakeets in their native range, particularly in South America, has been closely associated with human-induced changes in land use, such as the planting of exotic tree species and agricultural development (Bucher and Aramburú 2014). Beyond their native range, Monk Parakeets have successfully established populations in Europe (Strubbe and Matthysen 2009), Asia (Postigo et al. 2016), North America (Minor et al. 2012), and other regions, supported by their ability to adapt to both urban and agricultural landscapes. These range expansions have not only provided new nesting opportunities for Monk Parakeets, but have also increased the availability of the parakeet nests for other cavity-adopting species, offering valuable resources for these cavity adopters in both native and introduced ranges (Tracey and Miller 2018).

Kestrels face significant population declines in North America (Bird and Smallwood 2023), influenced by multiple factors such as habitat loss, predation, and climate change. Although the availability of suitable cavities can be a key limiting factor for cavity-nesting species (Newton 1994, Cockle et al. 2010), its role in kestrel population trends varies regionally and may not be the primary driver of decline (Smallwood et al. 2009, McClure et al. 2017). Research has shown that Monk Parakeet nests offer additional benefits, such as thermal insulation (Caccamise and Weathers 1977) and potential cooperative defense against predators, making them valuable nesting sites for other species (Hernández-Brito et al. 2021). Although kestrels exhibit flexibility in their nest site selection, their re-use of certain cavities may indicate high-quality sites or stable environments (Aitken et al. 2002, Martin 2004). However, cavity reuse can also increase predation risk, particularly in easily accessible sites (Brightsmith 2005). Moreover, cavity reuse potentially leads to accumulation of ectoparasites over time, which may negatively affect nesting success (Loye and Carroll 1998).

In this study, we describe natural nest sites used by American Kestrels in the caldén (*Neltuma caldenia*) forests of central Argentina during three consecutive breeding seasons. Our objectives were to: (1) evaluate the proportion of nesting attempts across different substrates (excavated cavities, non-excavated cavities, Brown Cacholote nests, and Monk Parakeet nests); (2) analyze the reuse of these cavities; and (3) evaluate whether cavity reuse is associated with their physical characteristics or the presence of Monk Parakeets in the same nest.

METHODS

Study Area. We studied kestrels in Parque Luro Provincial Reserve (36°54′S, 64°16′W; Fig. 1), located in La Pampa province, Argentina. The reserve lies within the Caldén district of the Espinal Ecoregion. Covering 73.5 km^2, it is the main protected area dedicated to the conservation of caldén woodlands in La Pampa. The area is characterized by savanna-like forests dominated by *caldén* trees, with *algarrobo dulce* (*Neltuma flexuosa*) although less abundant, and a diverse understory of shrubs, including *piquillín* (*Condalia microphylla*) and *molle* (*Schinus fasciculatus*; Cabrera 1994). Beyond the reserve, the surrounding landscape has been extensively transformed by agricultural expansion, with original forest habitats replaced by croplands containing wheat, maize, and sunflower, and pastures for livestock production (Viglizzo and Jobbágy 2010, Subsecretaría de Ambiente 2021; Fig.1).

Field Methods. We searched for kestrel pairs and occupied cavities between September and February of three breeding seasons (2016/17, 2017/18, 2018/19). We conducted searches on foot on trails through wooded areas and by car along roads. Kestrels often perch in visible, open areas such as tree tops, fence posts, or utility poles, where they hunt or monitor

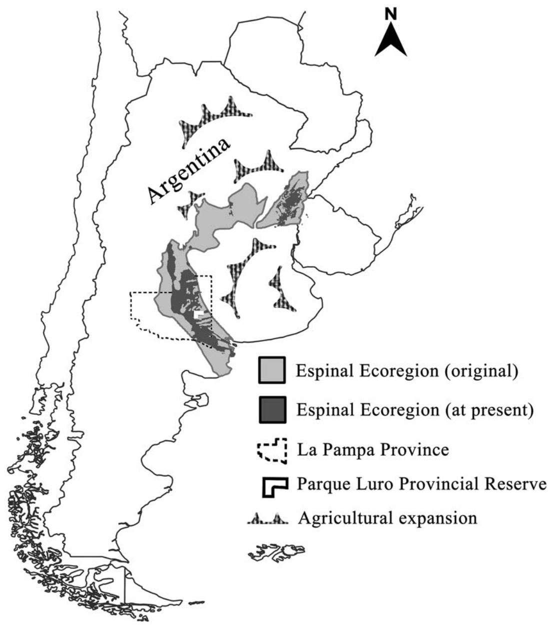

Figure 1. Geographical location of the Parque Luro Provincial Reserve, La Pampa, Argentina, showing the original and current extent of the Espinal ecoregion, as well as the agricultural expansion (Adapted from Viglizzo and Jobbágy 2010 and Subsecretaría de Ambiente 2021).

their territories (Toland 1986, Smallwood and Bird 2020). We repeated surveys (≥3) along these routes when necessary, which, combined with this species' tendency to occupy conspicuous perches, aided us in their detection and monitoring (Miller and Brown 2023). Once kestrels were spotted, we used binoculars or spotting scopes to follow them to their nests. We continued visiting territories until nests were located. Anthropogenic structures housing Monk Parakeet nests were also highly visible, which likely increased their detectability compared to smaller or concealed tree cavities.

In addition to natural cavities, 24 nest boxes were present in the study area, installed as part of other research projects (Orozco and Grande 2016). However, this study exclusively focused on natural cavities, and no data were collected on the use of nest boxes. This approach allowed us to analyze the role of natural nesting resources for American Kestrels in an environment with a potential abundant cavity availability (López et al. 2024).

We defined a nesting attempt as any case in which there was evidence of nesting activity, meaning that at least one member of a kestrel pair entered the cavity on ≥3 occasions or when eggs or nestlings were observed during the breeding season. To confirm occupancy when nests were not directly accessible, we used ladders, climbing equipment, and telescoping poles with cameras (Luneau and Noel 2010). In some cases, we used indirect cues, such as food deliveries or fledgling activity near the nest entrance, to assess reproductive status. We classified cavities used by kestrels as: excavated, non-excavated, Brown Cacholote nests, and Monk Parakeet nests. Cavities with multiple nesting attempts in the same season were counted only once to avoid pseudoreplication in the analyses (i.e., if a pair laid a second clutch after a failed attempt).

We measured cavity characteristics, including orientation, inclination (angle of the cavity entrance relative to the horizontal plane), height, depth, and entrance dimensions (estimated as elliptical based on the minimum and maximum diameters of the entrance). We used tools including a hypsometer, Suunto MC-2 compass, and measuring tapes to obtain these measurements, and we recorded each nest location with a GPS receiver.

Statistical Analysis. To analyze the proportion of cavity types used, we employed contingency tables. To explore relationships between cavity reuse and the physical characteristics of the cavities (e.g., orientation, depth, inclination, entrance area), we conducted a principal component analysis (PCA). For nest orientation, the angles were transformed into radians and decomposed into their cosine and sine components to account for cardinal directions (east–west and north–south; Berens and Velasco 2009).

We set a significance level of $\alpha = 0.05$ for all statistical analysis. Data are presented as mean ± SE (range). We performed all statistical analyses with RStudio version 2023.06.1 (R Core Team 2023) and PAST version 4.11 (Hammer et al. 2001, Everitt and Hothorn 2010).

RESULTS

Nesting Attempts and Types of Cavities Used. Over three breeding seasons, we documented 74 nesting attempts in natural nest sites; our finding corresponded to an occupied cavity for every American Kestrel pair occupying a territory that we found. Nesting attempts occurred in 49 unique cavities with some cavities reused in subsequent seasons. The proportion of nesting attempts by nest type included 74.3% in Monk Parakeet nests, 10.8% in excavated cavities, 9.5% in non-excavated cavities, and 5.4% in Brown Cacholote nests (Table 1). The proportion of attempts in parakeet nests was

Table 1. Structural characteristics of cavities occupied by American Kestrels in Parque Luro Provincial Reserve, Argentina. For measured variables ($n = 49$), values are presented as mean ± SE (range).

Variable (and Year)	Excavated Cavity	Non-excavated Cavity	Brown Cacholote Nest	Monk Parakeet Nest	Total or Mean + SE (range)
No. of nesting attempts (2016/17)	3	3	3	16	25
(2017/18)	3	1	1	20	25
(2018/19)	2	3	0	19	24
No. of unique cavities (all years)	8	5	4	32	49
No. of reused cavities (all years)	0	1	0	15	16
No. of nesting attempts in reused cavities (all years)	0	2	0	23	25
Nest height (m) (all years)	4.0 ± 5.1 (2.0–6.1)	4.1 ± 6.6 (2.8–6.3)	6.8 ± 6 (5.4–8.1)	8.2 ± 4.9 (4.0–15.9)	7.0 ± 4.2 (2.0–15.9)
Nest depth (cm) (all years)	69.3 ± 17.5 (23–180)	65 ± 7.3 (46–87)	40 ± 8.9 (25–60)	34.7 ± 1.4 (20–60)	43.9 ± 3.7 (20–180)
Nest entrance area (cm^2) (all years)	59.4 ± 6.9 (41.0–103.6)	71.1 ± 14.2 (37.7–117.8)	38.9 ± 4.5 (28.3–50.2)	52.6 ± 2.6 (28.3–102.1)	54.5 ± 2.6 (28.3–117.8)

significantly higher than in all other cavity types ($\chi^2 = 96.49$, $P < 0.01$). Comparisons among the remaining cavity types (excavated, non-excavated, and Brown Cacholote nests) showed no significant differences in use frequency ($P > 0.05$ for all pairwise comparisons).

Cavity Reuse and Influence of Parakeet Presence. Kestrels reused 16 different cavities across the study period: 15 of these were in Monk Parakeet nests and one was in a non-excavated cavity (Table 1). When kestrels reused Monk Parakeet nests, parakeets were simultaneously occupying other chambers in 87% of the cases ($n = 13$).

Cavity Characteristics. Monk Parakeet nests were found in both anthropogenic structures ($n = 11$; e.g., electric poles, radio antennas) and in trees. Among trees, *caldén* hosted 19 Monk Parakeet nests, three Brown Cacholote nests, eight excavated cavities, and four non-excavated cavities. *Algarrobo dulce* contained two Monk Parakeet nests, one Brown Cacholote nest, and one non-excavated cavity. The cardinal orientation of the cavities varied depending on their type, and the overall inclination across all cavity types was $-48° \pm 3.8°$ ($-89° - 32°$; Fig. 2). The remaining general average characteristics (height, depth, and area of entrance) are presented in Table 1. None of these characteristics showed significant associations with cavity use and reuse (Table 2). The PCA similarly found no strong relationships between specific cavity characteristics and the likelihood of reuse by American Kestrels (Fig. 3). The first two components (PC1 and PC2) explained 50.3% of the total variance; the variables height, depth, inclination, and entrance area contributed the most to PC1, while orientation (sine and cosine) and entrance area had a strong influence on PC2 (Fig. 3; Table 2).

DISCUSSION

We found that Monk Parakeet nests play a substantial role in the breeding ecology of the American Kestrel in the *caldén* forest. Nearly three-quarters of the nesting attempts occurred in Monk Parakeet nests, a significantly higher proportion compared to other cavity types. Although the interaction between these species has been known for decades (Martella et al. 1985), previous studies have shown that kestrels typically rely on excavated or non-excavated cavities for breeding in natural contexts (e.g., de La Peña 2013, Salvador 2014). The absence of comparable studies in other regions where the two species coexist makes it challenging to determine whether this reliance is novel or has been underreported elsewhere. Given the ecological complexities of natural nesting substrates, studying cavity-nesting species in their natural environments is essential for understanding their breeding strategies and interactions (Bonaparte et al. 2024). Our results highlight the importance of Monk Parakeet nests as a key site resource for the American Kestrel in the *caldén* forest.

Our findings suggest that cavity reuse may play an important role in kestrel nesting strategies, particularly regarding selection of cavity type. Monk Parakeet nests were the cavities most frequently reused by kestrels across the three breeding seasons of our study. In most cases, the presence of Monk Parakeets in other chambers of the same nest appeared to promote kestrel cavity reuse. This cohabitation may be

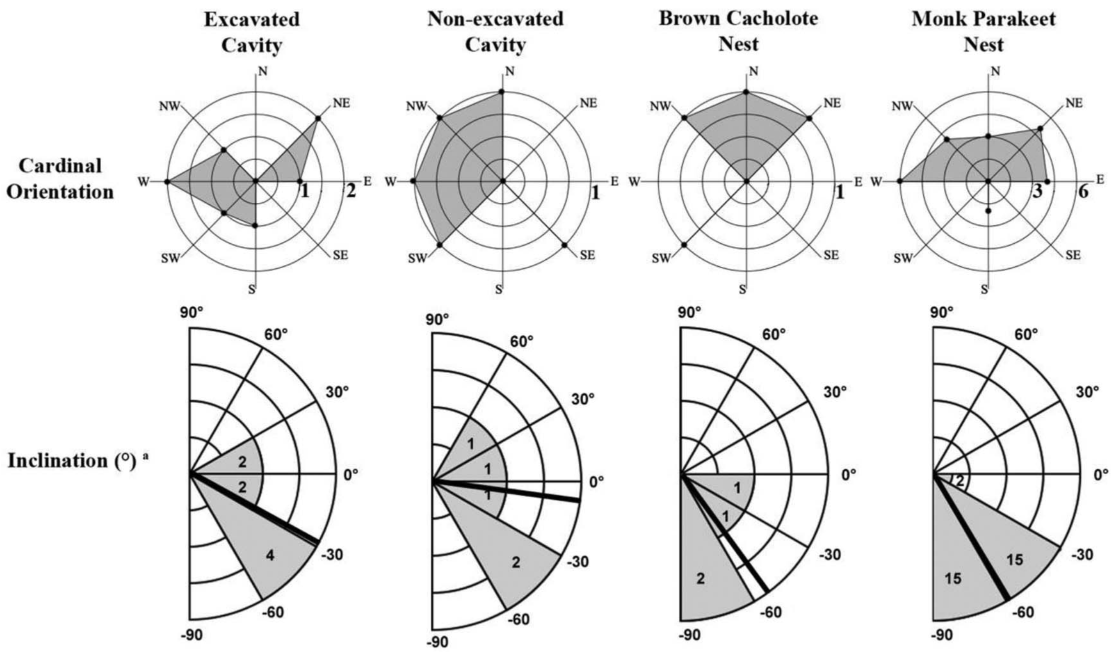

Figure 2. Cardinal orientation and inclination of entrances of unique cavities (n = 49) used all years by American Kestrels in Parque Luro Provincial Reserve, Argentina. Top panel: radial grid lines indicate frequency scale. Bottom panel: numbers indicate sample size (n) in each 30° interval. Bold black line indicates the mean value.

driven not only by the availability of nests but also by ecological benefits associated with this interaction. Although we did not evaluate the quality or stability of the environment, or assess ectoparasite impacts (Loye and Carroll 1998, Aitken et al. 2002, Martin 2004), factors including the microclimatic advantages of Monk Parakeet nests and predator deterrence may explain this dynamic (Caccamise and Weathers 1977, Hernández-Brito et al. 2020). Evidence shows that kestrels can prey on Monk Parakeets in some contexts, suggesting a complex relationship between these species that balances mutual benefits with occasional predation (Celis-Diez 2016). The frequent reuse of parakeet nests by parakeets alongside kestrels suggests that the benefits for parakeets outweigh the risks. This interaction may indicate a facultative mutualism, where kestrels benefit from nest availability while Monk Parakeets appear to tolerate their presence. However, further research is needed to determine whether this association consistently provides reciprocal advantages or if it aligns more closely with other ecological interaction, such as commensalism or neutral tolerance.

We found that the physical characteristics of cavities used by kestrels vary widely, with Monk Parakeet nests being the only ones found on artificial structures, while other cavities are located in native trees. The high visibility of Monk Parakeet nests, due to their large and conspicuous design often situated in open areas or on anthropogenic structures, likely facilitates their detection by both kestrels and researchers (Steenhof and Newton 2007, Hernández-Brito et al. 2021). This characteristic may partially explain their frequent use as nesting sites. During our fieldwork, we

Table 2. Principal component (PC) analysis of the characteristics of cavities used and reused by American Kestrel in Parque Luro Provincial Reserve, Argentina.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	2.0	1.1	1.0	0.8	0.7	0.5
% variance explained	32.7	17.6	15.9	14.0	11.8	8
Height	−0.6	−0.1	−0.3	0.3	−0.1	0.7
Depth	0.5	−0.1	−0.2	0.3	0.8	0.2
Inclination	0.5	0.1	0.6	−0.1	−0.2	0.6
Entrance area	0.4	0.4	−0.4	0.6	−0.5	−0.1
Sine	−0.3	0.3	0.6	0.6	0.2	−0.1
Cosine	−0.1	0.9	−0.1	−0.4	0.2	0.1

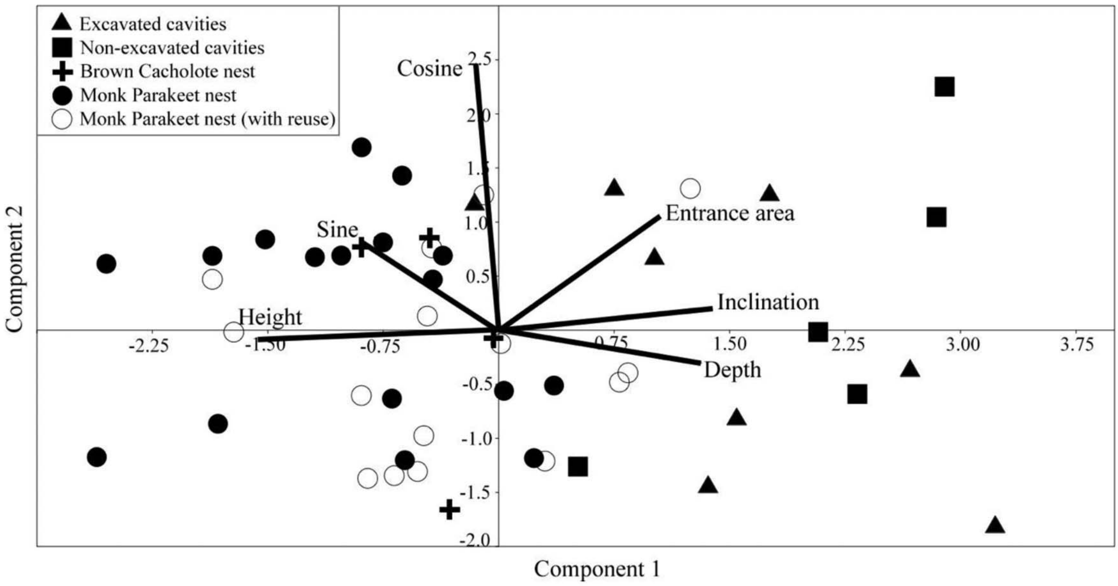

Figure 3. Principal component (PC1 and PC2) analysis of the characteristics of cavities used and reused by the American Kestrel in Parque Luro Provincial Reserve, Argentina.

conducted extensive surveys across Parque Luro, ensuring the detection of kestrel pairs and their nesting sites. We are confident that this effort allowed us to locate the nesting sites of all kestrel pairs occupying territories, following methodologies similar to those described by Miller and Brown (2023). Furthermore, despite the availability of nest boxes in the area, previous studies (Orozco and Grande 2020) have shown that their occupancy rates in forested areas like Parque Luro are significantly lower than in agricultural lands, likely due to the greater availability of natural cavities, such as Monk Parakeet nests. Similarly, López et al. (2024) reported that natural cavity density in Parque Luro is significantly higher than in managed landscapes, reinforcing the idea that kestrels in this area have abundant natural nesting options. Given this high availability of natural cavities, our study specifically aimed to assess nest site selection under natural conditions, without the confounding influence of artificial structures. However, in areas with varying levels of nest box availability, the relative selection of Monk Parakeet nests might differ. Future studies incorporating artificial nesting structures could further explore how kestrels balance their selection between natural and artificial options, particularly in landscapes where cavity availability is more limited.

The factors influencing cavity reuse by kestrels may extend beyond physical attributes, as our PCA did not reveal any significant relationships between cavity characteristics and their reuse. This suggests that broader ecological dynamics, such as proximity to food resources or interspecific interactions, may play a more critical role in nest-site selection and/or re-use (Forstmeier and Weiss 2004, Greenwood and Dawson 2011, Hernández-Brito et al. 2021). These results highlight the complexity of kestrel nesting behavior, pointing to factors that go beyond structural advantages. Further research is needed to evaluate whether kestrel-parakeet cohabitation provides other ecological benefits.

Kestrels demonstrate remarkable adaptability to local conditions, such as the presence of Monk Parakeets, which create communal nests that provide valuable nesting opportunities for other species (Salvador 2014, Hernández-Brito et al. 2021). Human activities, landscape changes, and the introduction of nonnative species have further influenced the availability of nesting sites, enabling kestrels to utilize both communal nests and artificial structures (Tracey and Miller 2018, Smallwood and Bird 2020). Current evidence suggests that American Kestrel populations are shaped by multiple factors, including food resources, predation pressure, and landscape changes, with nest site availability playing a variable role depending on the local context (Smallwood et al. 2009, McClure et al. 2017). Although significant population declines have been reported in

North America, the species remains widely distributed in South America. For example, in Argentina, it is classified as not threatened (Aves Argentinas 2017). These regional differences highlight the need for further studies on kestrel populations in South America. Understanding these variations in kestrel populations is crucial, particularly in the context of human-altered landscapes. For instance, the colonization of Monk Parakeets in nonnative regions, such as North America and Europe, has introduced new nesting opportunities for kestrels and other cavity-adopting species (Hernández-Brito et al. 2021). Of course, introductions of nonnative species may result in negative change to ecosystem dynamics, such as competition for nesting sites and displacement of native species.

The transformation of the *caldén* forest, driven by agricultural expansion and land use changes (Viglizzo and Jobbágy 2010, Graesser et al. 2015), has undoubtedly influenced the nesting ecology of avian species in the forest beyond. Although Monk Parakeets have historically been part of the Espinal avifauna, their presence in the region predates these landscape transformations (Burgio et al. 2020). Anthropogenic change has increased the availability of nonnative trees, artificial structures, and foraging opportunities, enabling both species to adapt and thrive in modified landscapes (Bucher and Aramburú 2014). As Monk Parakeet populations continue to expand, their nests may increasingly support kestrel populations in anthropogenic landscapes, potentially offsetting some habitat limitations. Nevertheless, the ongoing decline of kestrel populations in some regions, particularly in North America, underscores the importance of understanding alternative nesting strategies and balancing potential benefits and risks (Bednarz and Therrien 2023). Addressing these knowledge gaps through future research could inform conservation actions that help mitigate the challenges faced by this charismatic raptor.

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