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Research paper

Influence of captive breeding, release date and sex on the natal philopatry of the lesser kestrel *Falco naumanni*

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Abstract

Influence of captive breeding, release date and sex on the natal philopatry of the lesser kestrel Falco naumanni. The lesser kestrel *Falco naumanni* is a facultative colonial falconiform whose breeding range stretches across the entire Palaearctic. As with other pseudo-steppe birds, the lesser kestrel has experienced a sharp decline in western Europe over the last decades, spurring conservation actions. We compared natal philopatry of captive versus wild-bred individuals and the effect of release date on philopatry by comparing return data of captive- and wild-bred kestrels from 13 colonies between 2004 and 2019. We found that wild-bred kestrels show significantly stronger philopatry than their captive-bred counterparts, possibly due to the lack of parental influence experienced by the latter during their first days. No relationship was detected between release date and natal philopatry. Future studies should focus on factors affecting the philopatric behaviour of lesser kestrels bred in captivity, which could in turn improve their captive breeding and release strategy.

Key words: Captive breeding, Conservation, Hacking, Pseudo-steppe birds, Natal philopatry, Release date

Resumen

Influencia de la cría en cautividad, la fecha de liberación y el sexo en la filopatría del cernícalo primilla, Falco naumanni. El cernícalo primilla, *Falco naumanni*, es un falconiforme colonial facultativo cuya área de reproducción abarca todo el Paleártico. Al igual que otras aves pseudoesteparias, esta especie ha sufrido una marcada reducción demográfica en Europa occidental en las últimas décadas, lo que ha impulsado medidas de conservación. Analizamos la filopatría de ejemplares criados en cautividad y silvestres, así como el efecto de la fecha de liberación comparando datos del retorno de cernícalos criados en cautividad y silvestres a 13 colonias entre el 2004 y el 2019. Observamos que el comportamiento filopátrico era significativamente más acentuado en las aves silvestres que en las criadas en cautividad, posiblemente debido a la falta de influencia parental que esas últimas experimentan durante los primeros días de vida. No se encontró ninguna relación entre la fecha de liberación y el comportamiento filopátrico. Los futuros estudios deberían centrarse en los factores que influyen en el comportamiento filopátrico de los cernícalos criados en cautividad, lo cual podría mejorar la zoocría de esta especie y la estrategia de liberación.

Palabras clave: Cría en cautividad, Conservación, *Hacking*, Aves pseudoesteparias, Filopatría, Fecha de liberación

Introduction

Pseudo-steppe with grasses and annuals includes a variety of xeric, thermophilic and mostly open Mediterranean perennial and annual grasslands, found primarily in Portugal and Spain but also in France, Italy, Greece, Cyprus and Malta (European Commission 2007). Iberian pseudo-steppes are listed among the European landscapes with the highest value for biodiversity conservation since they are home to the main European populations of steppe birds (Santos and Suarez 2005) whose distribution is restricted to fragmented habitat patches, making them particularly sensitive to environmental disturbances (Estrada et al 2004). In 1915, steppes stretched over 73,500 km^2 in Spain, covering around 14.5 % of the country (Reyes-Prósper 1915). Today, the optimal habitat for steppe birds has decreased due to an interplay of rural land abandonment and changes in traditional agricultural practices in favour of industrial activity, the service sector, the transformation of drylands into irrigated lands and the expansion of intensive agriculture (González et al 2001, Estrada et al 2004, Carrete et al 2006, Martínez and Calvo 2006, SEO/BirdLife and BBVA Foundation 2008). This trend is similar in other European countries, increasing concern regarding the conservation of steppe birds at a continental scale since the end of last century (Goriup and Batten 1990). More recently, climate change has also been claimed to exert a negative impact on their habitat quality (Sarà 2010, Ortego 2016) as suggested by demographic parameters such as nest occupancy and success rate along with the mean number of fledged chicks per successful nest (e.g., Rodríguez and Bustamante 2003).

The lesser kestrel *Falco naumanni* (Falconidae) is a steppe bird whose breeding range stretches from western Europe across the Palaearctic to the Far East, while its wintering grounds are mostly located in Sub-Saharan Africa (Cramp and Simmons 1980) (fig. 1A). In the Iberian Peninsula, this small migratory raptor inhabits pseudo-steppe environments generally linked to traditional agricultural activities (Atienza and Tella 2004, Carrete et al 2006, SEO/BirdLife and BBVA Foundation 2008). Other than the above-mentioned threats typical of steppe environments, the Spanish population of lesser kestrel has shown a decrease in nesting sites used by breeding pair due to looting of tiles, building restorations, and collapses of rural and historical buildings such as barns or old churches (González et al 2001, Atienza and Tella 2004, Calabuig et al 2007, SEO/BirdLife and BBVA Foundation 2008, Negro et al 2020). The decreasing abundance of Arthropod prey, mostly Orthoptera, associated with changes in land use is also a a cause of the local decline of the lesser kestrel in recent years (Aparicio et al 2022). Taken together, these threats warranted its inclusion in the Red Book of Birds of Spain (Atienza and Tella 2004) and in the 'Regional Catalogue of Endangered Species' in Madrid Region (law 18/1992, of March 26) as Vulnerable and Endangered species, respectively.

An important aspect of the lesser kestrel biology - in line with that of most birds (Greenwood 1980) - is its strong philopatric behaviour (e.g., Negro et al 1997, Serrano et al 2001, Alcaide et al 2009), with individuals showing high fidelity to either their birth colony (natal philopatry) or that where they made an attempt to breed in the previous year (breeding philopatry). As with other migratory birds (Kokko et al 2006), male kestrels arrive first from the wintering areas, establish themselves in a nesting site and compete with other males for the best territory to attract females (Calabuig et al 2008). In birds, males are expected to exhibit stronger philopatry than females, since they benefit from a greater knowledge of the territory, while females tend to disperse and be more selective (Greenwood 1980, Greenwood and Harvey 1982). Nevertheless, while a number of studies show sex differences in philopatry (Serrano and Tella 2003, Serrano et al 2003, 2005), others do not (Negro et al 1997, Serrano et al 2001), this also being the case of Madrid Region (Goded-Millán and Garcés-Toledano 2013). Noteworthy, the most comprehensive work (probably) performed to date shows that lesser kestrel philopatry to the natal colony is low in certain environmental contexts (Serrano et al 2003), with a number of confounding factors such as population density and between-colony distance modulating dispersal (Serrano and Tella 2003, Serrano et al 2001, 2005). However, provided that natal philopatry may vary on a context-dependent basis in this species and that this is important from a conservation point of view, it is not sufficiently clear what happens in heavily urbanised areas such as Madrid Region.

In light of the local conservation status, the wildlife recovery centre and veterinary hospital GREFA (Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat), an NGO based in Majadahonda (Madrid, Spain), dedicates part of its efforts to preserving this species in Madrid Region (fig. 1B, 1C). In this framework, GREFA developed the project 'Corridors for the Lesser Kestrel', which aims to recover colonies of this species by placing nestboxes in extant buildings and infrastructures such as silos. GREFA has also been carrying out a captive breeding programme since 1994. The effectiveness (primarily in terms of breeding success and offspring viability but also success in establishment of new self-sustaining populations) of ex situ strategies for the lesser kestrel has already been demonstrated on several occasions, both in Spain and in other countries such as France (Lopo and Gutiérrez 1998, Pomarol et al 2002, Lelong 2009, Martín et al 2009a, 2009b, Polo 2009, Rodríguez et al 2013).

While some studies comparing captive-bred and wild-bred raptors found no differences in the use of diverse nesting substrates or in movement patterns (Faccio et al 2013) or home range size (Jobson et al 2021) of captive-bred individuals, behavioural alterations were detected in others. In particular, the lack of parental influence on released birds has been invoked to explain their lower survival by impairing the ability to search for food, socialise with conspecifics and avoid predators (Brown et al 2006), and their reproductive success (Liu et al 2020). On the other hand, lower dispersal and mobility patterns may relate to opportunities of returning for food and shelter (Fajardo et

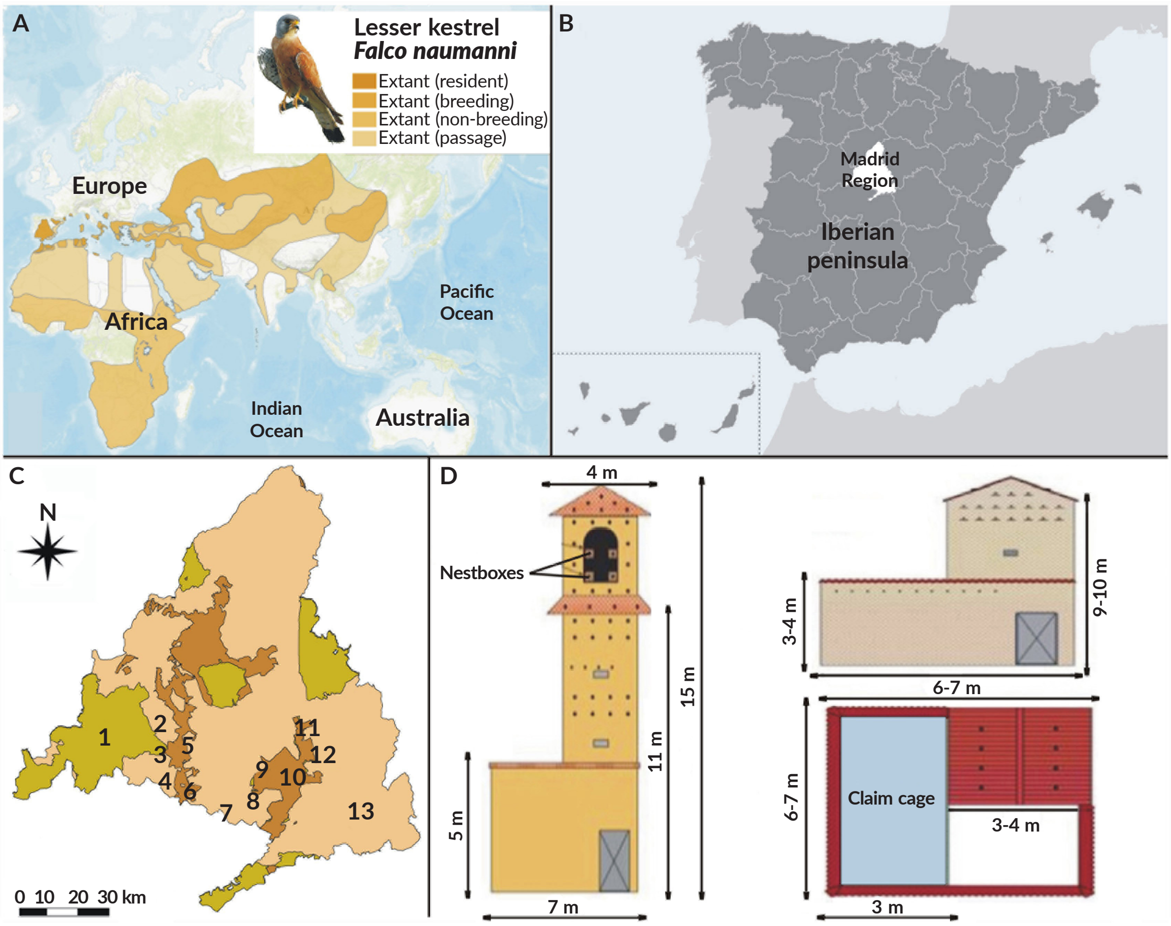

Fig. 1. A, lesser kestrel breeding and winter range (IUCN 2023). B, location of Madrid Region (white shape) within Spain and the Iberian Peninsula. C, map of Madrid Region with the municipalities where the study colonies are located (1, Navas del Rey; 2, Quijorna; 3, Sevilla la Nueva; 4, Navalcarnero; 5, Villaviciosa de Odón; 6, Batres; 7, Torrejón de Velasco; 8, Pinto; 9, Perales del Río 10, La Marañosa; 11, San Fernado de Henares; 12, Arganda del Rey; 13, Villarejo de Salvanés). Special Protection Area (SPA) are indicated in green, other protected areas in brown and non-protected areas in salmon. D, general plans of the two types of breeding towers used in this study.

Fig. 1. A, área de reproducción e invernada del cernícalo primilla (IUCN 2023). B, ubicación de la Comunidad de Madrid (indicada en blanco) dentro de España y la península ibérica. C, mapa de la Comunidad de Madrid con los municipios donde se encuentran las colonias (1, Navas del Rey; 2, Quijorna; 3, Sevilla la Nueva; 4, Navalcarnero; 5, Villaviciosa de Odón; 6, Batres; 7, Torrejón de Velasco; 8, Pinto; 9, Perales del Río; 10, La Marañosa; 11, San Fernando de Henares; 12, Arganda del Rey; 13, Villarejo de Salvanés). Las zonas de especial protección para las aves [ZEPA] están indicadas en verde; otras zonas protegidas en marrón, y las zonas no protegidas en salmón. D, esquema general de los dos tipos de primillares usados en este estudio.

al 2000). However, no differences in natal philopatry between wild and reintroduced populations of captive-bred individuals emerged in other studies (e.g., Jenny et al 2018). For this reason, it is crucial to assess how captive breeding affects the philopatric behaviour of a given species of conservation interest. The number of insightful behavioural studies on the lesser kestrel over the last decades points towards a limited influence, if any, of captive breeding (Goded-Millán and Garcés-Toledano 2013) and, more specifically, release date, body condition and chick hierarchy (Serrano et al 2003: cf. their ontogenic social subordination hypothesis) on the philopatry and natal dispersal of this species. On the basis of these considerations, juveniles of roughly the same age are expected to show a similar philopatric behaviour, which is why GREFA captive-bred chicks are released at a certain age (when they are similar in size) so that at the time of release they all are equally competitive (Serrano et al 2003). At the beginning of 2001, GREFA drew up a plan for the creation of a ring of new artificial colonies in Madrid Region called breeding towers (fig. 1D and fig. 1s, 'breeding towers general structure' in supplementary material), where hundreds of lesser kestrels have been born (Ortego 2016), reducing the negative effects associated with inbreeding (or genetic drift), which are known to affect reproductive success (Ortego et al 2007b, 2009) and parasite resistance (Ortego et al 2007a).

The main goal of the present study was to evaluate the effect of captive breeding on philopatric behaviour in individuals from different breeding populations. Secondly, we aimed to assess the influence of other factors such as release date and sex of captive-bred individuals on philopatry. More specifically, we tested the following hypotheses: 1) natal philopatry of wild-bred individuals will be stronger than that of captive-bred individuals, which may suffer behavioural changes as observed in other captive-bred raptors (e.g., Fajardo et al 2000, Brown et al 2006); 2) the release date of captive-bred individuals has no effect on the natal philopatry based on the 'Ontogenic social subordination hypothesis' (Serrano et al 2003); 3) there are no differences between sexes in terms of philopatric behaviour, both being equally likely to settle in their colony of origin (natal philopatry: Negro et al 1997, Serrano et al 2001, Goded-Millán and Garcés-Toledano 2013).

Material and methods

Study area

The study relied on GREFA data collected between 2003 and 2019 (with ringing performed between 2003 and 2018) in thirteen breeding towers in Madrid Region (fig. 1B, 1C), all located in seemingly optimal areas for the lesser kestrel. The predominant climate is temperate Mediterranean with tendencies towards the continental Mediterranean climate in certain areas (Dirección General de Biodiversidad y Recursos Naturales, Consejería de Medio Ambiente, Ordenación del Territorio y Sostenibilidad 2019). This climate is characterised by an intense arid or semi-arid period between May and September, maximum rainfall around November and frequent frosts in the winter months (Vide and Olcina 2001), while the landscape consists of a mosaic of crops (especially cereals), wastelands and herbaceous grassland formations typical of the Mediterranean biome (Loidi 2017).

Study individuals

During the 16-year study period (2003-2019), 304 (8.92 %) individuals were sighted out of the 3,409 (of which 1,284 were wild-bred and 2,125 were captive-bred) that had been previously (2003-2018) ringed. Of these, 151 were wild-bred individuals born in different colonies, while 145 were captive-bred individuals. Birds had been released between 2003 and 2018 (table 1s in supplementary material) in groups of similar size (three to four nestlings) at the age of 18 days. Individuals with delayed development were released two days later. Hacking is the release of juveniles during the dependency stage (i.e., ca. 18 days) when they receive supplementary food until they can fly and become independent (Martínez and Calvo 2006, Martín et al 2009b). This practice is intended to generate imprinting or bonding similar to that of the nestlings hatched and grown naturally in the same colony, thus favouring their return for breeding upon sexual maturity attainment (Calabuig et al 2008, Martín et al 2009b). Twelve wild-bred birds were tagged with GPS. We assumed that the marking of individuals did not influence the results or affect bird survival or behaviour, as ascertained in the lesser kestrel (Hiraldo et al 1994, Rodríguez et al 2009a, 2009b) and other ecologically similar small falcons (e.g., Vekasy et al 1996).

Data collection

All the nestlings born or released into the different breeding towers were marked before reaching one month of age with two rings: a metal ring, that was readable only when handling the bird, and a PVC ring with a three-digit numerical, alphabetic or alphanumeric code, and distinguishable by colour (blue, white, red or green). The ringing of the nestlings and their monitoring as fledglings (including ring reading through a telescope from a hide and, at a later stage, nest check: see table 2s in supplementary material) until migration from May to August. Returned individuals and breeding pairs were tracked by reading PVC rings from a hide with a telescope for three days during the reproductive season in their colonies, which were monitored sequentially as soon as the first arriving kestrels were detected from March to July or August. For the sake of clarity, spotting occasionally an individual at a given moment in a given colony was not deemed sufficient to consider it as settled therein. To assess if this was the case, its behaviour was monitored looking for supporting evidence such as nest choice, territory defense (primarily by males), courtship, and mating or reproduction. Overall, the monitoring effort was, on average, of one week per colony (table 2s in supplementary material), although this time might vary depending on colony size and observer experience. Data collection took place from 08:00 am to 12:00 pm, during the hours of lesser kestrel maximum activity. Adults of both sexes are easily distinguishable in the field as opposed to juveniles, which cannot be sexed until they are one-year old and undergo the first post-juvenile moult. For the purpose of this study, kestrels sighted in the colony of origin were referred to as philopatric, as opposed to those sighted in other colonies, and referred to as dispersing. In our study, natal philopatry was indistinguishable from breeding philopatry, as no individual that returned to its colony of origin was later sighted in a different colony. In other words, there were no cases of individuals acting as philopatric and dispersing during different years. However, three birds (one captive-bred and two wild-bred) were sighted in colonies other than the one of origin in subsequent years and were considered dispersing. For the 304 rings read during the study, the following information was recorded: 1) hatching year (and of release for captive-bred individuals); 2) rearing status (i.e., wild-bred versus captive-bred); 3) colony of origin (either birth or release colony); 4) sex; 5) colony of sighting; and 6) date(s) of sighting. For captive-bred individuals, release date (i.e., one of the two fortnights of May, June or July) was also recorded. For the sake of clarity, we could not establish the sex of seven individuals or the return colony of one individual (since it was sighted in two different colonies without knowing in which one it settled); therefore, they were excluded from downstream analyses. The size of the sighting colony in terms of reproductive individuals per year was also considered in the analysis to control its effect. Thus, the explanatory variables were origin, sex, and release date (only for captive-bred individuals), while the response variable was the binomial philopatric/dispersing behaviour of individuals. A dispersal matrix

Table 1. Generalized Linear Model coefficients with the lowest AIC (349.58), that includes rearing status, sex, year of birth and sighting colony as predictors of natal philopatry (n = 296). This model shows significant differences in terms of the rearing status of lesser kestrels, with wild-bred individuals being more prone to return to the same colony (null model deviance: 375.89 with 295 df; residual deviance: 323.58 with 283 df).

Tabla 1. Coeficientes del modelo lineal generalizado con el AIC más bajo (349,58) que incluye como predictores de la filopatría el tipo de cría, el sexo, el año de nacimiento y la colonia de avistamiento (n = 296). Este modelo muestra diferencias significativas entre los dos tipos de cría de los cernícalos primillas, ya que los ejemplares silvestres son más propensos a regresar a la misma colonia (desviación del modelo nulo: 375,89 con 295 grados de libertad; desviación residual: 323,58 con 283 grados de libertad).

	Estimate	Standard error	*Z*-value	Pr(>|z|)
Intercept	175.068	101.306	1.728	0.840
Rearing (wild-bred)	0.980	0.311	3.149	0.002
Sex (male)	0.432	0.272	1.591	0.112
Year of birth	-0.087	0.050	-1.739	0.082
Batres	0.338	1.537	0.220	0.826
Navalcarnero	0.649	1.474	0.440	0.660
Navas del Rey	1.388	1.555	0.893	0.372
Perales del Río	0.931	1.520	0.612	0.540
Pinto	1.168	1.480	0.789	0.430
Quijorna	0.147	1.493	0.098	0.922
Sevilla la Nueva	0.214	1.694	0.126	0.899
Torrejón de Velasco	-17.109	723.791	-0.024	0.981
Villaviciosa de Odón	1.341	1.544	0.869	0.385

was built for both wild-bred and captive-bred individuals (tables 3s and 4s in supplementary material).

Statistical analysis

Generalized Linear Models (GLMs) were performed to assess the occurrence of differences in philopatric behaviour, the dependent binomial variable, between groups of different rearing status, release date, or sex. Year of birth, colony of origin, colony of sighting and size of this colony in the year of sighting were also used as possible predictors in the GLMs. Fisher's exact tests were also performed to assess the relationship between variables, and the results obtained were consistent with those obtained in the GLMs. For the sake of clarity, the significance level considered at all times was 95 %. To perform the statistical analysis, RStudio 2023.12.1.402 software was used to work with R programming language 4.3.1.

Results

Out of the 296 lesser kestrels surveyed (8.68 % of those initially ringed), 198 (66.89 %) showed philopatric behaviour by returning to the same colony where they were born or where they were released. In contrast, 98 (33.11 %) showed dispersal to a different colony to that of origin. Regarding our first hypothesis, which claims that lesser kestrel philopatric behaviour is influenced by the rearing status (i.e., wild versus captive-bred), the number of wild-bred philopatric individuals was slightly higher than that of captive-bred individuals (111 wild-bred versus 87 captive-bred), while the number of captive-bred dispersing individuals was slightly higher than that of wild-bred individuals (40 wild-bred versus 58 captive-bred). The majority of the GLMs performed showed that the rearing status of the lesser kestrels influences natal philopatry, with wild-bred individuals being more prone to return to the same colony than wild-bred individuals (p = 0.002, n = 296; table 1). Even though the size of the sighting colony showed no relation with natal philopatry in GLMs, some of the models showed significant differences between colonies of origin or sighting, indicating that the environment that surround the colonies could be more important than the size of the colony. Regarding the second hypothesis, which suggests that philopatric behaviour is not influenced by the release date of captive-bred kestrels, the differences in the number of individuals released in each fortnight were large, more than the half of all those released in June (91 of 145 individuals: fig. 2A; table 5s in supplementary material). GLMs with the lowest AIC value showed no relationship between release date of the captive-bred lesser kestrels and natal philopatry ($p \geq 0.158$, n = 145; table 2). Regarding the third hypothesis, which suggests that philopatric behaviour is not influenced by sex, all the GLMs performed showed that this has no influence on the natal philopatry (p = 0.112, n = 296; table 1), although the proportion of philopatric males was slightly higher than that of females among dispersing individuals (i.e., 63.24 % for females vs 70 % for males). However, GLMs performed separately on females and males showed that in females (n = 136) the rearing status is a possible predictor of philopatric behaviour in more models than in males (n = 160). This could point to certain differences between sexes that we would detect with a larger sample size. Specifically, captive-bred females were the only group in which we observed an equivalent number of philopatric and dispersing individuals (i.e., 37:30), while in the other groups the philopatric behaviour was more frequent, although to a different extent (fig. 2B; table 6s in supplementary material).

Discussion

We collected return data of both wild-bred and captive-bred lesser kestrels in Madrid Region over a 15-year period in order to explore the relationship between rearing status and natal philopatry and the underlying drivers.

We found that natal philopatry in the 296 ringed birds tracked (66.89 %) in the present study was comparable to that obtained in a similar study between 2002 and 2010 (63.60 %: Goded-Millán and Garcés-Toledano 2013). Considering that some of the study colonies are the same in both these studies, this congruence suggests that general philopatric trends did

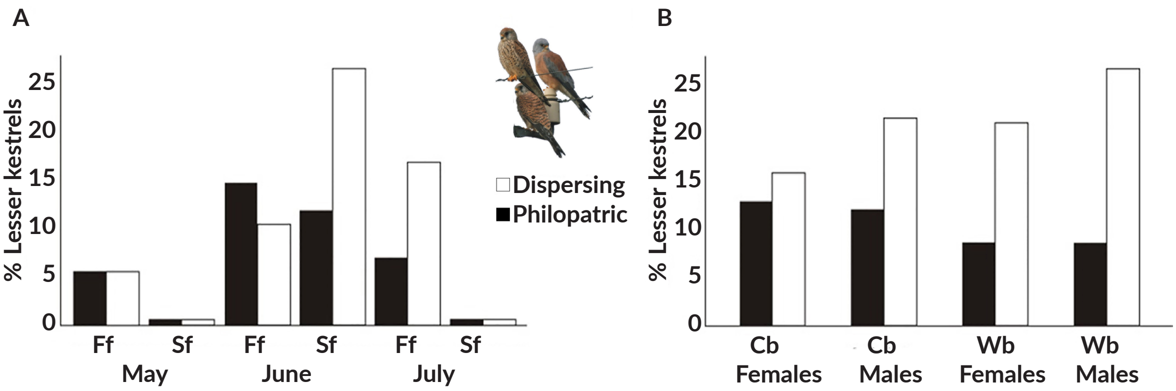

Fig. 2. A, release timeline of philopatric and dispersing lesser kestrels between 2004 and 2019: first half of May, n = 8; second half of May, n = 2; first half of June, n = 35; second half of June, n = 38; first half of July, n = 26; second half of July, n = 2). B, philopatric and dispersing lesser kestrels across captive-breeding females (n = 50), captive-breeding males (n = 61), wild-breeding females (n = 66) and wild-breeding males (n = 82). Ff, first fortnight, Sf, second fortnight; Cb, captive-bred; Wb, wild-bred.

Fig. 2. A, calendario de liberación de cernícalos primilla filopátricos y no filopátricos entre 2004 y 2019: primera quincena de mayo, n = 8; segunda quincena de mayo, n = 2; primera quincena de junio, n = 35; segunda quincena de junio, n = 38; primera quincena de julio, n = 26; segunda quincena de julio, n = 2). B, comportamiento filopátrico y no filopátrico entre las hembras criadas en cautividad (n = 50), los machos criados en cautividad (n = 61), las hembras silvestres (n = 66) y los machos silvestres (n = 82). Ff, primera quincena, Sf, segunda quincena; Cb, criado en cautividad; Wb, silvestre.

not vary over almost two decades. Noteworthy, Negro et al (1997) found similar rates in Andalusia (southern Spain; 57 %: Negro et al 1997). Nevertheless, other studies reported markedly lower rates in natal philopatry (~17 %: Serrano and Tella 2003, 2012, Serrano et al 2001, 2003). This body of information corroborates the previous suggestion, namely, that variation in natal philopatric behaviour could be a consequence of factors related to the number of colonies, their size, their proximity, or the environment where they are found (Serrano et al 2003, Goded-Millán and Garcés-Toledano 2013). Incidentally, we observed a lower dispersal rate once kestrels had settled in a colony, suggesting a stronger influence of breeding than natal philopatry, in accordance with other studies on this species (Serrano et al 2001, 2003, Serrano and Tella 2012) and other bird dispersal studies (cf. Greenwood 1980, Greenwood and Harvey 1982).

Effect of rearing status on natal philopatry

A previous study aimed at assessing the influence of rearing status on the philopatry of the species (Goded-Millán and Garcés-Toledano 2013) detected no differences. The main contribution of this study to lesser kestrel conservation lies in showing that the philopatric behaviour of captive-bred individuals was significantly lower than that in wild-bred birds. This observation is valuable to redirect captive breeding methodology and release strategies, which should be aimed at promoting connectivity between extant colonies and the establishment of new colonies. Considering that the contribution of individuals from breeding programs may be limited in this respect to their dispersal patterns, it is necessary to continue investigating the specific causes behind these differences and how to avoid them, delineating new strategies for the purpose of conservation actions. Captive-breeding may pose challenges to the successful implementation of conservation programs. As an example, a lower survival rate was found in captive-bred aplomado falcons *Falco femoralis* - a species which is phylogenetically close and ecologically similar to the lesser kestrel - released through hacking, seemingly due to the lack of parental influence. This would indeed jeopardise their ability to search for food and to adopt effective antipredator strategies, while also having detrimental effects on their social interactions (Brown et al 2006). Nevertheless, no compelling evidence was found in the Mauritius kestrel *Falco punctatus* for reduced survival among captive-bred and wild-bred individuals (Nicoll et al 2004).

Future studies should assess whether parental influence also affects lesser kestrel dispersal by comparing individuals released through hacking with those released through fostering or direct adoption, which consists of introducing nestlings (or, possibly, eggs) into active nests with same-age (and, hence, size) resident offspring (cf. Bailey and Lierz 2017).

Effect of release date on natal philopatry

The relationship between release date of captive-bred lesser kestrels and their philopatric behaviour has not yet been empirically addressed. Here we showed that release date had no effect on natal philopatry. Noteworthy, the results obtained align with the 'ontogenic social subordination hypothesis' (Serrano et al., 2003), postulating that neither the body condition, nor the date of birth and hierarchy within the brood of chicks affected

Table 2. Generalized Linear Model coefficients with the lowest AIC (157.00) that includes the release date, colony of origin, sighting colony and the size of the sighting colony as predictors of natal philopatry (n = 145). This model shows no differences in terms of the release date of captive-bred lesser kestrels. (Null model deviance 195.17 with 144 df Residual deviance 105.00 with 119 df).

Tabla 2. Coeficientes del modelo lineal generalizado con el AIC más bajo (157,00) que incluye como predictores de la filopatría la fecha de liberación, la colonia de origen, la colonia de avistamiento y el tamaño de esta (n = 145). Este modelo no muestra diferencias significativas en cuanto a la fecha de liberación de los ejemplares criados en cautividad. (Desviación del modelo nulo: 195,17 con 144 grados de libertad; desviación residual: 105,00 con 119 grados de libertad).

	Estimate	Standard error	Z-value	Pr(>|z|)
Intercept	-14.739	5438.785	-0.003	0.998
First fortnight of May	-1.908	1.351	-1.413	0.158
Second fortnight of May	0.474	2.068	0.229	0.819
First fortnight of June	-0.833	0.977	-0.852	0.394
Second fortnight of June	0.284	0.829	0.342	0.732
Second fortnight of July	1.078	3.216	0.335	0.738
Batres	17.752	5438.785	0.003	0.997
La Marañosa	-1.909	8790.812	0.000	1.000
Navalcarnero	22.678	5438.785	0.004	0.997
Navas del Rey	16.206	5438.785	0.003	0.998
Perales del Río	19.365	5438.785	0.004	0.997
Pinto	-2.193	7131.114	0.000	1.000
Quijorna	23.798	5438.785	0.004	0.997
San Fernando de Henares	-2.078	6563.645	0.000	1.000
Sevilla la Nueva	18.281	5438.785	0.003	0.997
Villarejo de Salvanés	-1.377	6259.864	0.000	1.000
Villaviciosa de Odón	18.008	5438.785	0.003	0.997
Navalcarnero	-4.104	1.854	-2.213	0.027
Navas del Rey	0.175	1.128	0.155	0.877
Perales del Río	-1.918	1.444	-1.329	0.184
Pinto	-0.716	6563.645	0.000	1.000
Quijorna	-4.500	1.720	-2.616	0.009
Sevilla la Nueva	-2.966	1.701	-1.744	0.081
Torrejón de Velasco	-25.729	2848.905	-0.009	0.993
Villaviciosa de Odón	-0.860	0.885	-0.972	0.331
Sighting colony size	-0.120	0.079	-1.524	0.128

natal philopatry. In our study, released nestlings were of similar size, unlike what happens in a natural nest, so fledglings were arguably displaced by adults only.

We acknowledge that the statistical power of our study might be limited due to the low number of kestrels released on two of the six study fortnights in May and July (May: n = 2; July: n = 2), and future studies based on larger sample size are required. Nevertheless, our results suggest that release date is not a crucial factor to consider in captive breeding programs, since no effect on philopatry was detected. The limited effect of parental influence on dispersal rate might not be surprising in a long-distance migrant with a short parental dependency period (as opposed to non-migrant with longer ones: e.g., van Heezik et al 2009), but it is worth mentioning that in other migratory species some differences in return rate and reproductive output (such as in the mallard *Anas platyrhynchos*: Yerkes and Bluhm 1998) and wintering site fidelity (such as in the Asian houbara *Chlamydotis macqueenii*: Burnside et al 2017) have emerged between captive-bred and wild-bred individuals. Noteworthy, release date and timing of the year - other than habitat quality - may strongly affect the survival rate of reintroduced birds (as in the case of the crested ibis *Nipponia nippon*: Wang et al 2021, Li et al 2021, 2022), which calls for careful examination of their effects concerning any hacking-based conservation action.

Influence of sex on natal philopatry and combined effect of rearing status and sex

The absence of differences between sexes (regardless to the captive-bred or wild-bred origin) were consistent with previous studies (Negro et al 1997, Serrano et al 2001, Goded-Millán and Garcés-Toledano 2013). On the other hand, the GLMs carried out for each sex separately showed that different predictors could modulate male and female natal philopatry in different ways, which is in agreement with the majority of studies in birds (e.g., Greenwood 1980, Greenwood and Harvey 1982, Johnson and Gaines 1990), including some on the study species encompassing differences in colony availability, distribution, size and degree of intraspecific competition (Serrano and Tella 2003, Serrano et al 2003, 2005, Goded-Millán and Garcés-Toledano 2013). In Andalusia and Madrid Region colonies are much more isolated from each other than elsewhere. They are separated by patches of unfavourable landscape for the species, so natal dispersal might pose higher risks, which is reflected in similar trends for both sexes. Nevertheless, we observed subtle differences in philopatric behaviour between females and males depending on rearing status, with captive breeding seemingly inhibiting philopatric behaviour in females to a larger extent than in males. Noteworthy, a study on peregrine falcon *Falco peregrinus* found similar results in terms of asymmetry between sexes (Dennhardt and Wakamiya 2013). More specifically, females travelled the longest distances to disperse followed by captive-bred and wild-bred males, respectively. Our study found that both captive-bred and wild-bred kestrels showed no sex difference in their return type. This supports the view held by others that differences in philopatry may be explained by environmental factors (Negro et al 1997, Serrano et al 2001). Arguably, captive breeding alters philopatric behaviour for both sexes but exerts greater influence on females. For this reason, the third hypothesis of this study, which supports the absence of differences between sexes, cannot be rejected. On the other hand, the first hypothesis, which suggests that captive breeding reduces the level of philopatry, remains to be corroborated in future studies to assess the occurrence of differences between sexes. We should also acknowledge that some degree of permanent emigration outside the study area - a widespread problem in the study of dispersal of open populations with bird ringing and encounter data - could not be completely ruled out. Should this be the case, erroneous conclusions regarding the factors underlying dispersal rates and sexual asymmetries in philopatry rates may be drawn. Several solutions have been proposed to overcome this problem, most of which require additional data and advanced capture-mark-recapture modelling techniques. Nevertheless, should our results be unbiased, they would confirm the occurrence of differences in the philopatric behaviour of lesser kestrels from different sites of the Iberian Peninsula. In this respect, it is worth mentioning that differences in natal dispersal distances between golden eagle *Aquila chrysaetos* populations from north America were found to have a genetic basis (Murphy et al 2019). Thus, variation in the strength of selection on philopatry among regions could be responsible for the pattern detected, an explanation that could also apply to the lesser kestrel in Spain. Genome-wide investigations based on non-neutral genetic variation could help address this question.

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Author contributions
M Lorenzo-Vélez, performed fieldwork, carried out the statistical analyses and wrote the first draft of this manuscript; **AF Malo** carried out formal analyses and edited the manuscript; **F Garcés-Toledano** carried out fieldwork; **B Rodríguez-Moreno** conceived and designed the study, carried out fieldwork and edited the manuscript; **P Izquierdo-Cezón** conceived and designed the study and carried out fieldwork; **J Martínez-Dalmau** carried out fieldwork; **R García-Roldán** carried out fieldwork; **G Forcina** refined the figures and edited the manuscript.

Conflicts of interest
The authors declare that they have no competing interests.

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Supplementary material

Breeding towers general structure

Each study breeding towers has common general features. Its design always consists of three basic components: the concrete tower (8-10 m high) where the nests are, a claim cage and a courtyard (fig. 1D). The nests are made taking advantage of the empty space inside concrete blocks. Nestboxes (fig. 1s in supplementary material) are located on the inner side of the tower, which coincide with each of these outer holes. The number of nestboxes per breeding tower varies between twenty-one and one hundred and eighty; likewise, the size of each box may vary. The entrance hole to the nests is 6.5 cm in diameter, a size that allows lesser kestrels to enter while preventing the entrance of competing species. Inside, there is usually a base of fine sand 0.5 cm thick to facilitate breeding. The boxes have a small door to allow for nest inspection. Three of the study breeding towers do not follow this structure, since they were created from previously existing buildings to which nests were added. More specifically, Navalcarnero and Villarejo colonies were built from silos that were given a new use, while Torrejón de Velasco colony was settled in a 12th century castle that already hosted a small population of lesser kestrels.

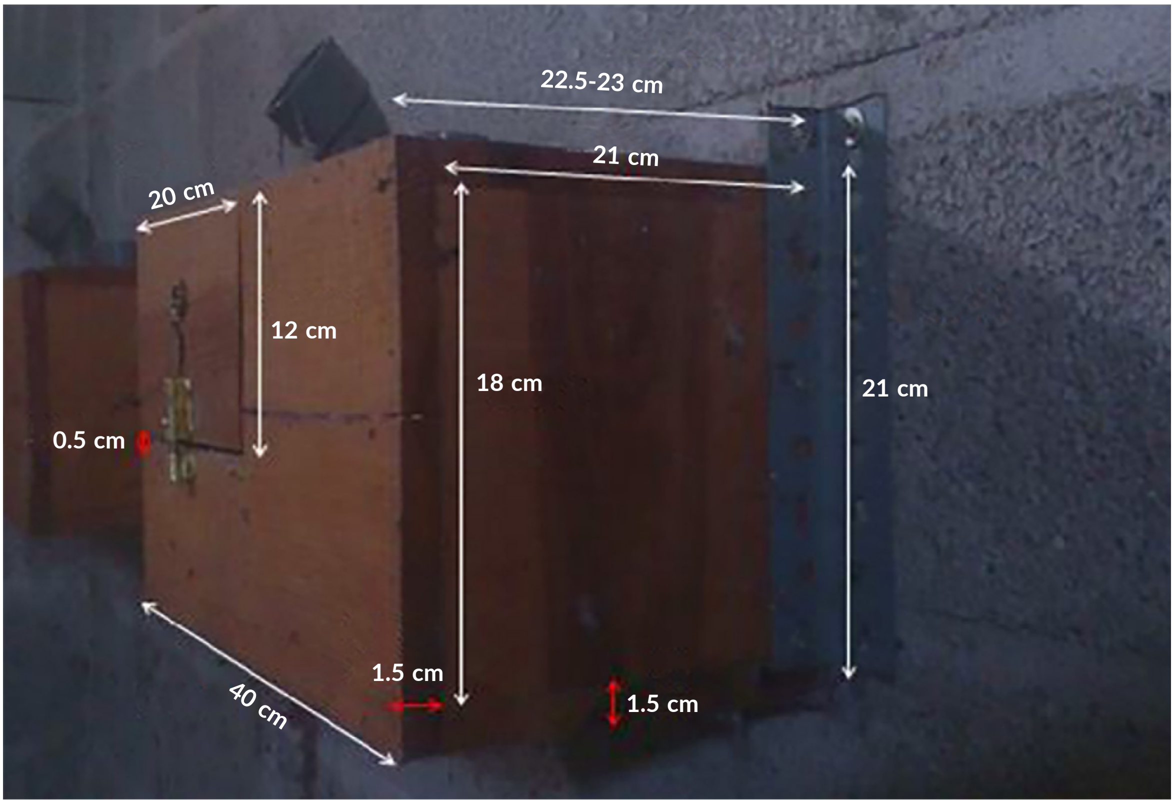

Fig. 1s. Measurements of standard nestboxes located in the breeding towers.

Fig. 1s. *Medidas de las cajas nido estándar ubicadas en los primillares.*

Table 1s. List of breeding towers according to the year of construction, indicating the number of lesser kestrels from breeding centres (n = 145) released by hacking between 2003 and 2018. A total of 67 females and 78 males (n = 145) were released. * No individual was released in Torrejón de Velasco, although there was dispersal to this colony of some individuals released elsewhere (n = 3), as well as of several individuals born in a different colony (n = 7). In fact, it is a special breeding tower because it was created from a pre-existing natural colony.

Tabla 1s. *Lista de los primillares por año de construcción, con el número de cernícalos procedentes de centros de cría (n = 145) y liberados por medio de hacking entre el 2003 y el 2018. En total, se liberaron 67 hembras y 78 machos (n = 145). * No se liberó ningún individuo en Torrejón de Velasco, aunque se registró dispersión a esta colonia de individuos liberados en otras colonias (n = 3), así como varios individuos nacidos en otras colonias (n = 7). De hecho, se trata de un primillar especial, ya que fue creado a partir de una colonia preexistente.*

Breeding towers	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total
Villaviciosa de Odón	2	5	1	3	3				10	2	6	1	1				34
Perales del Río			7	10												2	19
Monte de Batres					14	5		3		1	1						24
Navas del Rey						4	7	3		4							18
Pinto						2											2
Quijorna							1	8	3	1	1						14
Sevilla La Nueva								5	5	4	4	1					19
Navalcarnero										4	3		1				8
Villarejo de Salvanés											2						2
Arganda del Rey														1		1	2
La Marañosa														1			1
San Fernando de Henares															1	1	2
Torrejón de Velasco*																	0
Total	2	5	8	13	17	11	8	19	18	16	17	2	2	2	1	4	145

Table 2s. Monitoring effort made from the arrival of the first individuals until the end of the reproductive season between 2004 and 2019. Monitoring per colony may vary depending on its size and the experience of the observer.

Tabla 2s. *Esfuerzo de seguimiento realizado entre la llegada de los primeros ejemplares hasta el final del período reproductivo entre 2004 y 2019. El seguimiento de cada colonia puede variar en función de su tamaño y de la experiencia del observador.*

Monitoring type	Months	Duration per colony	Tasks	Comments
Pre-reproductive	April	2-3 consecutive days	Ring reading Pairs determination Determination of nests	Months depend on lesser kestrels arrival dates
Incubation	May-June	2-3 consecutive days	Collection of egg laying data Collection of chicks age data New pairs determination	Made from inside the breeding towers
Reproductive	July	2-3 consecutive days	Ring reading Ringing of the chicks	Months depend on egg laying dates

Table 3s. Number of wild-bred lesser kestrels expressed in a dispersing matrix (n = 151). Each row shows a colony of origin, while each column corresponds to the destination colony. Philopatric individuals are shown on the diagonal.

Tabla 3s. *Número de cernícalos primilla salvajes expresados en una matriz de dispersión (n = 151). Cada fila muestras una colonia de origen, mientras que cada columna se corresponde con la colonia de destino. En la diagonal se muestran los individuos filopátricos.*

	Navas del Rey	Quijorna	Sevilla la Nueva	Navalcarnero	Villaviciosa de Odón	Batres	Torrejón de Velasco	Pinto	Perales del Río	La Marañosa	San Fernando de Henares	Arganda del Rey	Villarejo de Salvanés
Navas del Rey	**8**	1	0	1	0	0	0	0	0	0	0	0	0
Quijorna	1	**11**	1	3	0	0	1	0	0	0	0	0	0
Sevilla la Nueva	0	0	**0**	0	0	0	0	0	0	0	0	0	0
Navalcarnero	0	0	0	**20**	0	0	0	0	0	0	0	0	0
Villaviciosa de Odón	0	2	0	0	**16**	5	3	0	0	0	0	0	0
Batres	0	2	0	2	0	**6**	1	0	0	0	0	0	0
Torrejón de Velasco	0	0	0	0	0	0	**0**	0	0	0	0	0	0
Pinto	1	0	0	0	0	0	0	**31**	5	0	0	0	0
Perales del Río	0	1	0	0	0	1	2	6	**18**	0	0	1	0
La Marañosa	0	0	0	0	0	0	0	0	0	**0**	0	0	0
San Fernando de Henares	0	0	0	0	0	0	0	0	0	0	**0**	0	0
Arganda del Rey	0	0	0	0	0	0	0	0	0	0	0	**1**	0
Villarejo de Salvanés	0	0	0	0	0	0	0	0	0	0	0	0	**0**

Table 4s. Number of captive-bred lesser kestrels expressed in a dispersing matrix (n = 145). Each row shows a colony of origin, while each column corresponds to the destination colony. Philopatric individuals are shown on the diagonal.

Tabla 4s. *Número de cernícalos primilla de cría en cautividad expresados en una matriz de dispersión (n = 145). Cada fila muestras una colonia de origen, mientras que cada columna se corresponde con la colonia de destino. En la diagonal se muestran los individuos filopátricos.*

	Navas del Rey	Quijorna	Sevilla la Nueva	Navalcarnero	Villaviciosa de Odón	Batres	Torrejón de Velasco	Pinto	Perales del Río	La Marañosa	San Fernando de Henares	Arganda del Rey	Villarejo de Salvanés
Navas del Rey	**11**	2	0	0	0	3	0	0	2	0	0	0	0
Quijorna	0	**12**	0	0	1	0	1	0	0	0	0	0	0
Sevilla la Nueva	0	8	**3**	7	0	0	1	0	0	0	0	0	0
Navalcarnero	0	0	1	**7**	0	0	0	0	0	0	0	0	0
Villaviciosa de Odón	3	4	0	2	**23**	2	0	0	0	0	0	0	0
Batres	0	1	1	1	7	**13**	0	0	1	0	0	0	0
Torrejón de Velasco	0	0	0	0	0	0	**0**	0	0	0	0	0	0
Pinto	0	0	0	0	0	0	0	**0**	2	0	0	0	0
Perales del Río	0	0	0	0	1	0	0	0	**18**	0	0	0	0
La Marañosa	0	0	0	0	0	0	0	1	0	**0**	0	0	0
San Fernando de Henares	0	0	0	0	0	0	0	1	1	0	**0**	0	0
Arganda del Rey	0	0	0	0	0	0	0	1	1	0	0	**0**	0
Villarejo de Salvanés	0	0	0	0	0	1	1	0	0	0	0	0	**0**

Table 5s. Contingency table showing the fortnight when captive-bred kestrels (n = 145) were released through hacking or country rearing and return type (i.e., philopatric and dispersing, depending on whether they returned or not to a colony other than the one of origin). Overall, 67 females and 78 males were released.

Tabla 5s. *Tabla de contingencia que muestra la quincena en que se liberaron los cernícalos criados en cautividad (n = 145) mediante hacking o crianza campestre y el tipo de retorno (es decir, filopátrico y no filopátrico, según regresaran o no a una colonia diferente a la de origen). En total, 67 hembras y 78 machos fueron liberados.*

	May		June		July		
	First fortnight	Second fortnight	First fortnight	Second fortnight	First fortnight	Second fortnight	Total
Dispersing	8	1	21	17	10	1	58
Philopatric	8	1	15	38	24	1	87
Total	16	2	36	55	34	2	145

Table 6s. Contingency table showing the sex (female or male) and origin (captive-bred and wild-bred) of the study individuals (n = 296) and return type (i.e., philopatric and dispersing, depending on whether they returned or not a colony other than the one of origin).

Tabla 6s. *Tabla de contingencia que muestra el sexo (hembra o macho) y el origen (cría en cautividad o en el medio natural) de los ejemplares de estudio (n = 296) y el tipo de retorno (es decir, filopátrico y no filopátrico, según regresaran o no a una colonia diferente a la de origen).*

	Captive-bred females	Captive-bred males	Wild-bred females	Wild-bred males	Total
Dispersing	30	28	20	20	98
Philopatric	37	50	49	62	198
Total	67	78	69	82	296