

Concerningly high breeding success rates for the European Starling after a recent invasion in the Neotropics

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Abstract

The European Starling is a highly invasive passerine that recently started to expand throughout South America. Despite its negative impacts on the native fauna, there are no reports of its breeding success, the population recruitment rate, or the factors affecting its nest success in these recently invaded natural habitats. In this study we monitored 100 European Starling nests in a native forest of central-eastern Argentina, during the 2020–2021 and 2021–2022 breeding seasons. We estimated the most common breeding parameters for the population (clutch size, number of fledglings, nest fate, nest survival) and measured nest-site features at different spatial scales to assess if they affected nest survival. Starlings used natural and woodpecker cavities, and nest initiation peak was in September. Successful nests produced ~ 3 fledglings and estimated nest success was 38%. Daily survival rates were negatively affected by nest-tree diameter at breast height. Nest survival was high compared to native cavity-nesting birds. Moreover, the breeding onset as soon as spring begins favors the successful occupancy of cavities by starlings. Here, we provide the first detailed information on the breeding parameters of the starling in South America, which is now available to help in the design of management programs. Given our results, in addition to their effective cavity usurpation behavior, we believe starlings represent a serious threat for endangered native cavity-nesting species and need to be controlled.

Introduction

The European Starling (*Sturnus vulgaris*, hereafter 'starling') is a highly invasive passerine, native to Eurasia and North Africa, that has invaded Oceania, North, Central and South America (Moulton et al. 2012, Cabe 2020). Its main threats to native fauna include unused cavity occupation (Mazgajski 2003), attacks to native birds (Jauregui et al. 2021) and usurpation of cavities used by cavity-nesting birds (Kerpez and Smith 1990; Koenig 2002; Frei et al. 2015). These behaviors have already been detected in South America (Rebolo Ifran and Fiorini 2010; Jauregui et al. 2021) where the invasion is recent (Codesido and Drozd 2021). Since the first reports in the mid-80s until 2004, the starling distribution in South America extended only to Buenos Aires city and its surroundings (Peris et al. 2005). However, the population grew exponentially and expanded through Argentina (map in Codesido and Drozd 2021), Brazil (Silva et al. 2017), Paraguay, Chile and Uruguay (distribution map provided by www.ebird.org, accessed 2 May 2022). Due to its invasive potential, studies regarding population growth rate are important to predict both the damage it might cause to native fauna and future impacts on (still) unreached areas. Accordingly, previous reports consider that this information is a key part in facing an ecological invasion and designing effective management programs (Groom et al. 2017, Ivanova and Symes 2019). However, this data is lacking for the starling invasion in South America.

Available information linked to the starling expansion in South America includes reports of its ecological function overlap with native species (Palacio et al. 2017; Codesido and Drozd 2021), its harmful effects on the native fauna (Rebolo Ifran and Fiorini 2010; Ibañez et al. 2017, Jauregui et al. 2021) or to its (under expansion) distribution range (Silva et al. 2017). Nevertheless, the relation between environmental characteristics and its breeding success and the basic nesting parameters of the species has not been

studied in natural habitats of South America. Only Ibañez (2015) partially described its nesting biology in an urban area and using artificial nest-boxes with no assessments of environmental influence on nest success. Data regarding the breeding success in natural habitats is crucial to understand the nature of the starling invasion and would help to develop management actions, as pointed out by local government authorities (MAyDS 2022; InBiAr 2022). A study including data on the starling nest-site characteristics and the factors influencing its breeding success would help to predict its future movements and contribute to design preventive actions against its advance. This is particularly important as the starling has still not reached areas inhabited by endangered cavity-nesting species (such as *Celeus galeatus* and *Amazona vinacea* in northern Argentina) which could be compromised by its arrival.

Our main objective is to report information of the European Starling reproduction in South America, focusing on a population breeding in a natural habitat of Argentina. We monitored starling nests during two consecutive breeding seasons (2020–2021 and 2021–2022) in an altered native forest of central-eastern Argentina. This native forest is being degraded due to human activity, resulting in the loss of forest mass and an increase in forest fragmentation (Arturi and Goya 2004). We estimated basic breeding parameters and measured nest-site characteristics at a local scale (cavity-tree) and a habitat scale (500 m around the nest) to assess if these features influenced nest survival.

Methodology

Study site and species

We conducted this study on a private farm ('Luis Chico', 35°20'S, 57°11'W; 8 m a.s.l.) located in the northeast of Buenos Aires Province, Argentina. The area is within the Pampas ecoregion, which has a temperate-humid climate, and is composed of grasslands and semi-open forests (locally known as 'talaes'). Forests represent ~ 15% of the total farm area and are arranged as connected patches or as isolated patches. Patches are mainly composed of the native *Celtis tala* and *Scutia buxifolia*. Other less abundant native species are *Erythrina crista-galli*, *Schinus longifolius*, and *Phytolacca dioica*. Exotic species, such as *Gleditsia triacanthos*, *Populus* spp., *Acacia melanoxylon*, and *Melia azedarach* (among others), are also well represented.

The starling is an omnivorous mid-size passerine that uses natural, artificial or woodpecker cavities to nest. Starlings typically rear two broods per season, with a clutch size of 4–6 eggs which are incubated for 12 days, producing 2–3 fledglings per breeding attempt (Kessel 1957; Korpimäki 1978).

Nest monitoring and nest-site features

We collected data during the 2020–2021 and 2021–2022 breeding seasons. We searched for nests intensively in every forest of the study area (~ 150 ha), throughout the entire breeding season. As breeding season length was not reported for the region, we searched for nests from early September (suggested breeding start given our own observations monitoring cavities during previous years) to early January (no new nests found after a two-week searching period). We found nests by either identifying

territories through adult activity (vocalizations, movements, displays), by listening to nestlings begging call (during the nestling stage) or by checking cavities prone to be used. Once found, we visited nests every day (during egg-laying and hatching stages), and every 3–10 days (during incubation and nestling stages). There were some nests ($n = 30$) which we could not monitor regularly (> 10 days between visits) and these were discarded for the nest survival analysis. We reached the cavity hole entrance by climbing through the branches and/or using a 5 m ladder and checked cavity content using a mirror (attached to a wire) and a small flashlight. We monitored all nests until nestlings fledged or the nest failed. We considered a nest successful when fledglings ≥ 1 . We considered a nest predated if all the eggs or nestlings (without being old enough to fledge) disappeared between two consecutive visits, and no parental activity was detected near the nest. We considered a nest abandoned if we saw the eggs during three consecutive visits or dead nestlings and no parental activity near the nest.

Once we confirmed that the nestlings had fledged or the nest had failed, we recorded cavity depth, inner diameter, entrance hole diameter and height from the ground. Cavity depth was defined as the distance between the lowest part of the hole and cavity floor and inner diameter was the distance between the cavity hole and the wall opposite to it. We followed Cockle et al. (2015) to record cavity hole diameter and considered cavity height as the distance between the lowest part of the hole and the ground. We estimated cavity volume as the product of cavity depth and cavity floor area (adapted from Wiebe and Swift (2001)), where cavity floor was modelled as a circle. Therefore, its area was $\pi \cdot r^2$; where r was half of the cavity diameter. We also determined the type of cavity used (natural, excavated by woodpeckers or Rufous Hornero *Furnarius rufus* nest), cavity-tree diameter at breast height (DBH) and species.

After the breeding season was over, we recorded forest features (cover and edge length) within a 500 m diameter circle (centered on the cavity-tree). We measured these through a SPOT6 satellite image (1.5 m spatial resolution) provided by the Comisión Nacional de Actividades Espaciales (CONAE) using QGIS 3.8 (QGIS Development Team 2018). By choosing an area this size, we aimed to account for landscape configuration. We considered forest cover as the number of pixels corresponding to tree canopies within the circle and edge as the pixels corresponding to stands (groups of trees of different size and age) or individual trees edges within the circle.

Breeding parameters

Each nest was assigned a clutch-initiation date (time of breeding), corresponding to the laying of the first egg. Clutch-initiation dates were determined directly for nests found during construction or egg-laying, or indirectly through backdating from hatching dates for nests found during incubation and from fledging dates for nests found during the nestling stage. For nests that were found during the incubation stage and failed in the following visit, we considered they were found in the middle of the incubation. For nests found during the nestling stage and that failed before fledging, we visually determined nestlings age to estimate clutch-initiation dates. We determined clutch size only for nests found during construction or egg-laying after we observed the same number of eggs during two consecutive days. Because cavity nest chambers are difficult to access, we were only able to take egg measurements (weight, length and width)

in three nests and nestling measurements (weight, wing, tarsus and bill) in one nest. We estimated egg volume following Hoyt (1979). Both eggs and nestlings were weighed using a Pesola scale (10 ± 0.1 g, 20 ± 0.2 g and 50 ± 0.5 g) and measured to the nearest 0.05 mm using Vernier calipers.

Hatching success was calculated by dividing the number of eggs hatched to the number of eggs that reached the hatching moment. The incubation period was estimated as the number of days elapsed from the laying of the last egg until the hatching of the last egg. Nestling period was estimated as the number of days elapsed from the hatching of the last egg until fledging. When nestlings were fully feathered and disappeared between two successive visits without predation signals, we assumed fledge date to be the midpoint between those visits. We estimated nest productivity as the number of fledglings divided by clutch size. We estimated breeding cycle duration as the days elapsed between laying of the first egg and fledging.

Analysis

We estimated daily nest survival rate (DSR) using the logistic-exposure model (Schaffer 2004). For this model, the observation unit is the time interval between visits and the response variable is coded as 1 = survived the interval and 0 = did not survive the interval. We built a null model (without covariates) to estimate constant daily survival rate. We then created models including simple effects (i.e., one variable per model) of cavity and habitat features on DSR. We also examined the linear and quadratic effects of time of breeding and the linear, quadratic and cubic effects of nest age to control for DSR influenced by temporal variables. We compared all models using Akaike's Information Criterion corrected for small samples (AIC_c). The model with the lowest AIC_c value was assumed to be the best supported model (Burnham and Anderson 2002). The cumulative probability that a nest had to survive was calculated by raising the daily survival rate to a power represented by nesting cycle duration (days elapsed between laying of the first egg and fledging). Reported values are means \pm SE.

Results

We found a total of 100 nesting attempts (39 in the 2020–2021 and 61 in the 2021–2022 breeding seasons). Four nests were found under construction, 28 during egg laying, 38 during incubation and 30 during the nestling stage. Twenty eight nesting attempts were in natural cavities, 70 were in woodpecker cavities and two were in Rufous Hornero nests. Trees bearing cavities were 43 *Celtis tala*, 16 *Populus alba*, six *Eucalyptus* spp., five *Melia azedarach* and four other tree species. Cavity, cavity-tree and habitat characteristics are summarized in Table 1. The earliest nesting attempt was initiated on 9 September and the last nestling fledged on 19 December (breeding season length = 101 days). Nest initiation peak occurred in September (Fig. 1). Time elapsed between two consecutive nesting attempts was 12.2 ± 0.4 days (range = 9–14, n = 7) for failed nests and 11.8 ± 0.5 days (range = 7–14, n = 13) for successful nests.

Table 1
 Measurements of cavities (n = 85), cavity-trees and the habitat surrounding them (n = 74) used by the European Starling to nest in forests of central-eastern Argentina.

Variable	Mean \pm SE (range)
Cavity height (m)	3.4 \pm 0.2 (0.7–7.6)
Cavity hole diameter (cm)	6.1 \pm 0.2 (3.5–11.0)
Cavity depth (cm)	31.9 \pm 0.9 (16.0–61.0)
Cavity diameter (cm)	12.8 \pm 0.5 (16.0–31.0)
Cavity volume (l)	4.8 \pm 0.5 (0.7–33.1)
DBH (cm)	47.7 \pm 2.4 (15.9–119.5)
Forest cover (ha)	6.4 \pm 0.7 (2.3–28.0)
Edge (km)	13.5 \pm 0.8 (5.3–34.2)

Clutch size was 4.7 ± 0.1 eggs (n = 4–6 eggs), and median clutch size was four eggs (n = 32 nests). Eggs were incubated for 13.8 ± 0.3 days (range = 13–15 days, n = 20 nests). Hatching success was 0.98 ± 0.02 (range = 0.75–1.00, n = 26 nests). There were 3.8 ± 0.2 nestlings per nest (n = 30 nests) and nestling survival was 0.76 ± 0.08 (range = 0.50–1.00, n = 21 nests). Nestlings remained in the nest for 19.2 ± 0.1 days (range = 18–20 days, n = 21 nests) and successful nests produced 2.7 ± 0.1 fledglings (range = 1–5 fledglings, n = 49 nests). Productivity was 0.57 ± 0.04 (range = 0.40–0.75) and breeding cycle lasted 34.7 ± 0.2 days (range = 33–37 days, n = 20 nests). Eggs and nestling measurements are summarized in Online Resource 1 and images are shown in Online Resource 2.

There were 49 successful nesting attempts, 31 depredated, 16 abandoned for unknown reasons (six during incubation and 10 during the nestling stage) and in four cases we were not certain of nest fate. Apparent nest success was 49%. Daily survival rate was 0.973 ± 0.003 (n = 392 intervals) and mean exposure period was 5.7 ± 0.4 days (range = 1–10 days). The cumulative probability that an average nest had to survive was 38% (0.973^{35}). The most supported model included a negative influence of DBH on DSR ($\beta = -0.66 \pm 0.2$ [Lower CI = -1.16, Upper CI = -0.3]; Table 2 and Fig. 2).

Table 2

Top fitting models explaining DSR variation in response to environmental variables on a European Starling population breeding in a forest of central-eastern Argentina. Df = degrees of freedom; logLik = log Likelihood; AIC_c = Akaike Information Criterion (corrected for small sample sizes); Δ = differences in AIC_c between models; w_i = AIC_c weight.

Variable	df	logLik	AIC _c	Δ	w_i
DBH	3	-70.8	147.7	0.0	0.96
Edge	3	-74.8	155.6	7.9	0.02
Cob	3	-75.8	157.9	10.1	< 0.01

Discussion

Our results indicate that European Starling breeding attempts in a recently invaded natural landscape of South America had a probability of success of ~ 38%. Though lower than the reported for its original distribution area (Korpimäki 1978; Mazgajski 2007), this breeding success is considerably higher than that of native cavity-nesting passerines in the same area. Particularly, it is higher than the ~ 25% of *Lepidocolaptes angustirostris* (Jauregui et al. 2019) and *Troglodytes aedon* (Llambias and Fernandez 2009) and doubles the ~ 19% of *Agelaioides badius* (De Mársico et al. 2010). In addition, the success rate here reported is similar to the 37% and the 45% of *Colaptes campestris* and *Colaptes melanochloros*, respectively (Cockle et al. 2015; Jauregui 2020), two native woodpeckers breeding in the area. Nevertheless, as the starling is double-brooded (Korpimäki 1978), its population growth rate doubles that of native woodpeckers, which are single-brooded. This breeding output suggests that this population is recruiting new individuals at a concerningly high rate compared to native cavity-nesting birds. Moreover, as the starling invasion in South America is recent, starlings may still be able to develop strategies to face a rather new predator, competitor and parasite communities after some adaptation time. If this is the case, breeding success could still reach even higher levels.

In addition to the high nest success rate found, the time elapsed between first and second broods was relatively short (~ 12 days), even for successful nests for which adults must attend recent fledglings. Although we cannot confirm broods in the same cavity belong to the same breeding pair because we did not band adults, cavity reuse by the same breeding pair for second clutches is frequent for the species (Royall Jr. 1966; Cabe 2020). Short time periods between clutches could be a way to avoid cavity occupation by other cavity-nesting species. Moreover, fledglings tend to form flocks shortly after leaving the cavity (Cabe 2020), which allows reduced parental care by the adults and favours energy investment in a new brood (Russell 2000). The period between broods was also short for failed first attempts. As an alternative explanation, reducing time between clutches (either failed or successful) prevents starlings from breeding during January and February, when bird nest success is considerably reduced in these latitudes (Segura and Reboreda 2012; Jauregui 2020).

The starling clutch initiation peaked in September, indicating a population synchronic start as previously reported for the species (Korpimäki 1978; Ojanen et al. 1979; Flux and Flux 1981). This is early compared to other cavity-nesting passerines within the area that start in late September and early October (Llambias and Fernandez 2009; de La Peña 2016; Jauregui et al. 2019). Hence, the early start in the breeding season could favour the starling breeding success by avoiding the competition with native species for cavity use. In addition, starlings used natural and woodpecker cavities for nesting, which are subject of competition between cavity-nesting species (Cockle et al. 2011). If cavity availability is a limiting factor, starlings can overcome this drawback as they have proven to be considerably successful cavity usurpers through aggressive behaviors (see Frei et al. 2015 and Jauregui et al. 2021 and articles there cited).

Starlings' nest survival was negatively influenced by cavity-tree diameter. We were surprised as this pattern contradicts the general idea that larger trees increase nest survival chance (Zhu et al. 2012; Nyrienda et al. 2016). Mature large trees have been in the ecosystem for a longer time, compared to smaller trees. Consequently, predators may search and find food in large old trees because they are used to it, similar to what was suggested for old vs. new cavities (Wiebe et al. 2007). Alternatively, among cavity-trees, the smallest individuals (i.e., with lower DBH) were mostly *Populus alba*. The trunk of this tree has few lateral branches and smooth-surfaced bark compared to *Celtis tala* trees (frequently used by starlings), which could make it inaccessible to terrestrial predators such as snakes or small rodents (AJ, *pers. obs.*). Nevertheless, during data exploration we were not able to find a significant relationship between cavity-tree species and nest fate. Whichever is the case, due to the contradiction of our result with previous ideas and the lack of clarity in our explanation, we suggest taking these results with caution and encourage the development of experimental studies that aim to clarify this pattern.

This study provides the first breeding data of the starling in South America, based on a population inhabiting a southern temperate forest of Argentina. Our results suggest that the starling exponential growth and expansion (Zufiaurre et al. 2016; Codesido and Drozd 2021) is favoured by a concerningly high breeding success. Information here reported regarding the starling nest-site characteristics can help to design management actions to mitigate the advance of this alien species (see management strategies in Feare et al. 1992 and Williams et al. 2019). If the patterns here reported (i.e., early and synchronic start, occupancy of natural and woodpecker cavities, and high breeding success) replicate in areas with threatened cavity-nesting species, consequences may be regrettable.

Declarations

Competing Interests. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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Data availability. Upon manuscript acceptance, authors are willing to share their data through a public repository.

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Figures

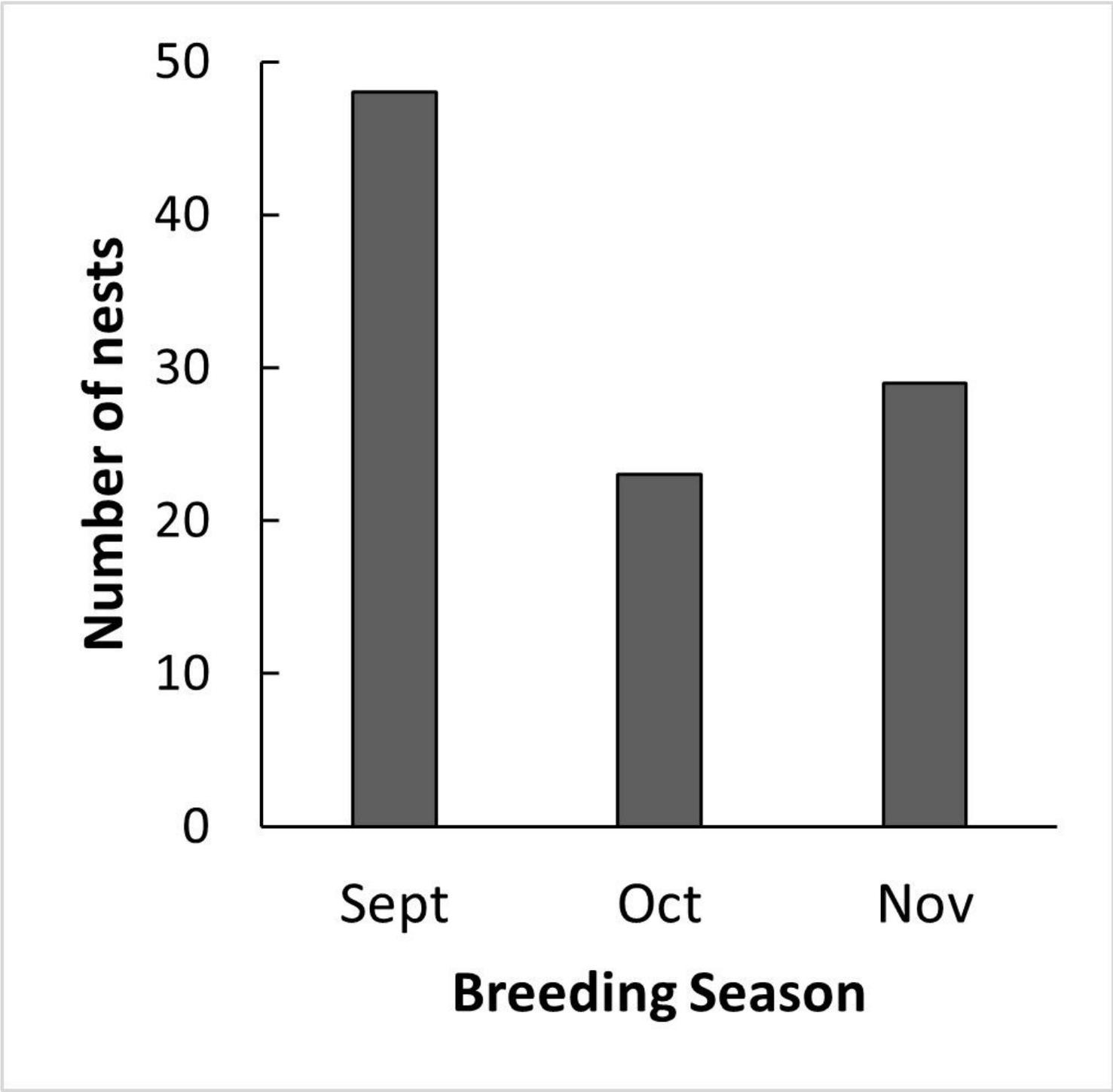


Figure 1

Temporal distribution of nest initiation by European Starling during two breeding seasons in a south temperate forest of central-eastern Argentina

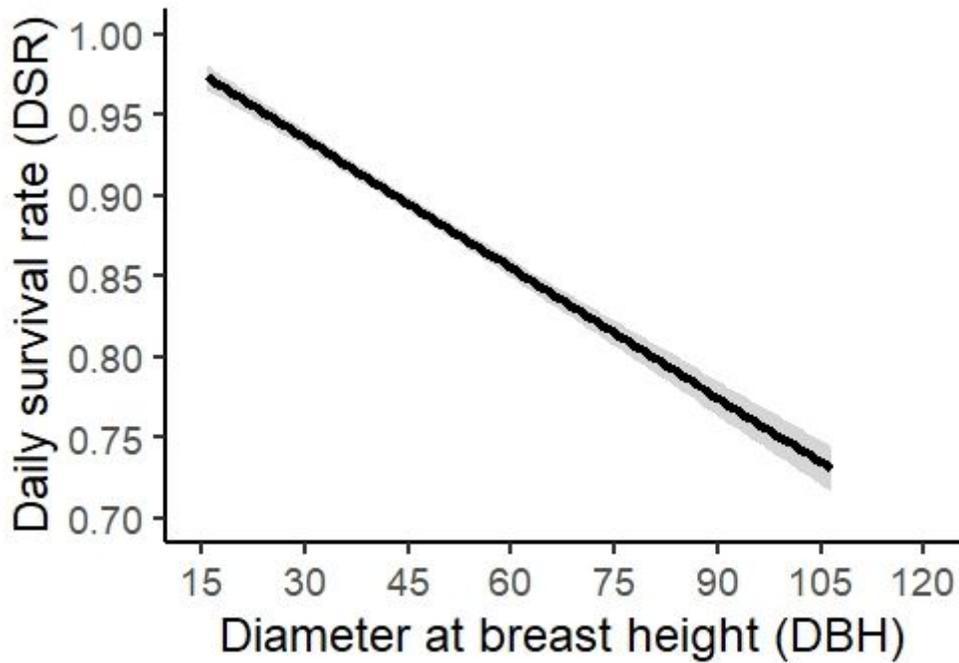


Figure 2

European Starling nest daily survival rate variation as a function of diameter at breast height (DBH) for a population breeding in central-eastern Argentina. Black solid line represents average relationship and grey areas surrounding it are the standard error

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