

Jauregui, A., P. A. Gerstmayr, M. A. Colombo, and L. N. Segura. 2023. High breeding success of the European Starling compared to native species in a recently invaded natural forest of South America. *Avian Conservation and Ecology* 18(1):12. <https://doi.org/10.5751/ACE-02401-180112>
Copyright © 2023 by the author(s). Published here under license by the Resilience Alliance.

Research Paper

High breeding success of the European Starling compared to native species in a recently invaded natural forest of South America

Adrian Jauregui¹ , Paula A. Gerstmayr¹ , Martin A. Colombo¹  and Luciano Noel Segura¹ 

¹Laboratorio de Ecología de Aves, Instituto de Limnología “Dr. Raúl A. Ringuelet,” CONICET-UNLP

ABSTRACT. Invasive species present numerous threats to ecosystems as they compete with other species for resources and displace them from their habitats. One of the most invasive birds is the European Starling (*Sturnus vulgaris*), which recently invaded and started to expand throughout South America. Despite its negative impacts on the South American native fauna, there is no information on its breeding success, the factors affecting it, and its population recruitment rate. 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 breeding parameters for the population (clutch size, number of fledglings, nest survival, among others) and measured nest-site features at different spatial scales to assess if they influenced nest survival and productivity. Starlings started breeding earlier than native species, used three cavity types (natural, woodpecker, and Rufous Hornero, *Furnarius rufus*), produced ~3 fledglings per successful nest, and had a 38% estimated nest success probability. Daily survival rates were negatively related to nest-tree diameter at breast height (DBH) but not related to landscape features. Nest survival and productivity were higher than those of native cavity-nesting birds. Moreover, starling successful occupancy of cavities earlier in the season may delay native cavity-nesting birds nest initiation dates, which negatively affects their breeding success. The inverse relationship between DBH and nest survival could indicate preservation of mature trees may help to reduce nest success rate but such a relationship deserves further study. The high reproductive rates in our study and effective nest usurpation by starlings shown elsewhere suggests that the effect of starlings on endangered native species needs further study and starlings may need to be controlled.

Succès de reproduction élevé de l'Étourneau sansonnet par rapport aux espèces indigènes dans une forêt naturelle récemment envahie en Amérique du Sud

RÉSUMÉ. Les espèces envahissantes représentent de nombreuses menaces pour les écosystèmes, car elles entrent en compétition avec les autres espèces pour s'approprier les ressources et les déplacent de leur habitat. L'Étourneau sansonnet (*Sturnus vulgaris*), un des oiseaux les plus envahissants, a récemment envahi l'Amérique du Sud et a commencé à s'y étendre. Malgré son effet négatif sur la faune indigène d'Amérique du Sud, il n'existe aucune information sur son succès de reproduction, les facteurs qui l'affectent et le taux de recrutement de sa population. Nous avons suivi 100 nids d'étourneaux dans une forêt indigène du centre-est de l'Argentine pendant les saisons de reproduction 2020-2021 et 2021-2022. Nous avons calculé les paramètres de reproduction de la population (taille de la ponte, nombre d'oisillons, survie du nid, entre autres) et mesuré les caractéristiques du site de nidification à différentes échelles spatiales afin d'évaluer si elles influençaient la survie du nid et la productivité. Les étourneaux ont commencé à nicher plus tôt que les espèces indigènes, ont utilisé trois types de cavités (naturelle, pic et Fournier roux, *Furnarius rufus*), ont produit ~3 oisillons par nid réussi et ont eu une probabilité de succès de nidification estimée à 38 %. Les taux de survie quotidiens ont été négativement liés au diamètre à hauteur de poitrine (DHP) de l'arbre de nidification, mais n'ont pas été liés aux caractéristiques du paysage. La survie du nid et la productivité étaient plus élevées que celles des oiseaux indigènes nichant dans des cavités. De plus, l'occupation réussie des cavités par les étourneaux plus tôt dans la saison retarde sans doute les dates d'initiation des nids des oiseaux indigènes nichant dans des cavités, ce qui affecte négativement leur succès de reproduction. La relation inverse entre le DHP et la survie des nids pourrait indiquer que la préservation des arbres matures contribuerait peut-être à réduire le taux de succès des nids, mais une relation de ce type mérite d'être étudiée plus amplement. Les taux de reproduction élevés de notre étude et l'usurpation effective des nids par les étourneaux, démontrée ailleurs, donnent à penser que l'effet des étourneaux sur les espèces indigènes menacées doit être étudié plus à fond et qu'il pourrait être nécessaire de contrôler les étourneaux.

Key Words: *biological invasion; invasive species; Neotropical region; nest survival; Sturnus vulgaris*

INTRODUCTION

Biological invasions represent serious threats to biodiversity conservation (Lowe et al. 2000, Levine 2008) because alien species may compete with native species for resources and cause declines in their populations. The transportation and introduction of an alien species to a new location is always the first step of the

invasion process (Blackburn et al. 2011). However, whether the last phase of the process (i.e., species established with a population that is growing and spreading) is reached depends on several factors. Facing new environmental conditions may be challenging for alien species, hence, ecological plasticity to adverse climate conditions may increase the chance of establishment and

spreading (Heger and Trepl 2003). Also, the nature of the native community plays a key role in the invasion process (Heger and Trepl 2003). The invasive species may be outcompeted for food and/or nest sites by native species (Levine 2008) or may not use novel foods (Lafleur et al. 2007). Breeding success of the alien species, which ultimately determines its recruitment rate, can also be reduced by local predators, competitors, and parasitism. Therefore, assessing the breeding success of alien species in recently invaded habitats is important to understand their invasive potential.

The European Starling (*Sturnus vulgaris*, hereafter “starling”) is a highly invasive cavity-nesting passerine, native to Eurasia and North Africa, that has invaded Oceania, and North, Central, and South America (Cabe 2020). Its invasive populations represent multiple serious threats (Linz et al. 2007), including cavity usurpation to native species (Kerpez and Smith 1990, Koenig 2002, Frei et al. 2015), occupation of available cavities (Mazgajski 2003), and attacks on native birds (Jauregui et al. 2021). Such behaviors have been causing problems to native species in the USA, South Africa, and Australia for the last 100 years (Wiebe 2004, Cabe 2020). In South America, the starling invasion is comparatively recent (Codesido and Drozd 2021), with the first records being from the early 80s in the city of Buenos Aires, Argentina (review in Peris et al. 2005). Until 2004, the distribution of the species was relatively restricted to the areas close to Buenos Aires (Peris et al. 2005). However, from that moment onward, the population grew and expanded exponentially (Zufiaurre et al. 2016). It currently occupies a core area of ~907.000 km² within the Buenos Aires province (Ojeda et al. 2022) and has already been recorded in many other provinces of Argentina (Codesido and Drozd 2021, Ojeda et al. 2022), and in other countries, including Brazil (Silva et al. 2017), Chile (Ojeda et al. 2022), Paraguay, and Uruguay (eBird 2022). In addition to their expansion, starlings are causing problems to the native fauna (Rebolo Ifran and Fiorini 2010, Ibañez et al. 2017, Jauregui et al. 2021) and to crops (Ibañez et al. 2016). However, not only are there no ongoing management programs to control the species, but there are no reports regarding habitat use, breeding success, or the factors affecting it. Only Ibañez (2015) reported that native parasites reduce nest success in artificial nest boxes in Buenos Aires. Understanding the determinants of reproductive success in natural habitats is crucial to predicting the risk the starling invasion may pose and will help to inform management actions (InBiAr 2022, MAyDS 2022). Studies regarding vital rates and population growth of starlings are important to predict potential impact of starlings on native fauna. This is particularly important because 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.

Cavity-nesting birds’ breeding success (i.e., nest survival and productivity) depends on several factors, the most important being predation, usurpation/competition with other species, and adults’ ability to successfully raise nestlings. Predation and usurpation rates depend on the influence of environmental features acting at different spatial scales (cavity, nest surroundings, and landscape; Cockle et al. 2015, Jauregui et al. 2022). For instance, high foliage cover may conceal the nest (Berl et al. 2014) although lower forest cover and higher fragmentation

may favor predators’ movements (Jauregui et al. 2022). Concurrently, nest location will impact food availability, which ultimately influences food delivery rates to nestlings given the distance adults must fly to find food (Segura et al. 2019). For starlings, reduction of habitat quality (the transformation of rangeland to cropland) may reduce breeding success because adults must fly farther distances from the nest to find food (Bruun and Smith 2003). In addition, Linz et al. (2007) claimed that limits to the population of North America may be caused by parasite-related mortality, though nothing was reported regarding relationships with environmental features. Starling population declines are related to brood size reductions through time in native populations of the species, but the causes of such reductions are not yet fully understood (Smith et al. 2012). Overall, there are still knowledge gaps regarding breeding success (i.e., nest survival and productivity) of invasive starling populations and its relationship with environmental features. An assessment of these relationships is important to understand (and a first step to predict) population dynamics.

Our main objective is to contribute the first assessments of the relationships between environmental features and breeding success (nest survival and productivity) of the European Starling in South America. In addition, we aim to contribute the first data on starling productivity in a natural habitat of South America, for which there is no previous report. To do so, we monitored starling nests during two consecutive breeding seasons (2020-2021 and 2021-2022) in a native forest of central-eastern Argentina and estimated basic breeding parameters. This forest is being degraded due to human activity, resulting in the loss of forest area and an increase in forest fragmentation (Arturi and Goya 2004). We measured nest-site characteristics at a local scale (cavity tree) and a landscape scale (500 m around the nest) that may influence nest survival and number of fledglings produced (as a proxy of productivity) based on the hypotheses in Zhu et al. (2012), Cockle et al. (2015), Jauregui et al. (2022), and articles therein cited. At a local scale, larger trees are less accessible for predators, and we expected to find a positive relationship between diameter at breast height (DBH) and breeding success. In addition, cavities with narrower openings prevent predators from reaching the nest chamber, and we predicted there would be an inverse relationship between cavity opening diameter and breeding success. At a landscape scale, starlings ideally need both forest fragments containing trees, which provide cavities to breed, and grasslands to search for food on the ground. Therefore, we predicted breeding success would be higher in forest fragments close to grasslands, expecting the interaction between forest cover and edge would influence breeding success.

METHODS

Study site and species

We conducted this study on a private farm (Luis Chico, 35°20′ 02.0″S, 57°11′31.1″W, 8 m a.s.l.) located in the northeast of Buenos Aires Province, Argentina. The area is located within the Pampas ecoregion, which has a temperate-humid climate, and is composed of grasslands and forests (locally known as *talares*). 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 relatively common.

The starling is an omnivorous mid-sized 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 forest stands (~25 patches) and individual trees within a 500-ha area of the farm and 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 identifying territories through adult activity (vocalizations, movements, displays), by listening to nestlings' begging call (during the nestling stage), and by checking cavities. 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 ($n = 30$) we could not monitor regularly (> 10 days between visits) and these were discarded from the nest survival analysis. There were 20 nesting attempts that appeared in cavities with recently finished attempts (range = 7-14 days between broods). Because we did not band adults, we cannot confirm whether these belong to the same breeding pair. However, given our intensive nest searching and monitoring methodology, which allowed us to survey most active nests (~90%) and evidence of starlings nesting twice in the same cavity for other populations (Royall 1966, Cabe 2020), we assume these were second broods from the same breeding pairs with a recently finished first attempt. 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 and found dead nestlings but no parental activity near the nest.

Once we confirmed the nestlings had fledged or the nest had failed, we recorded cavity depth, inner diameter, entrance hole diameter, and height from the ground. We defined cavity depth as the distance between the lowest part of the hole and cavity floor and inner diameter as 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 2003) in which the cavity floor was modeled as a circle. Therefore, its area was $\pi * r^2$ in which 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 of tree.

After the breeding season, we recorded forest features (cover and edge length) within a 500 m diameter circle (centered on the cavity tree). These variables allowed us to account for both landscape composition and configuration, respectively. Moreover, a circle this size captured landscape variation (assumed to influence predators' likelihood to find nests). Although we do not have home-range data from this population, we assumed this radius included the average home-range size based on evidence from other regions (Bruun and Smith 2003). We considered forest cover to be 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. We measured these on 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).

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 assumed they were found in the middle of the incubation stage. For nests found during the nestling stage 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 (mass, 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 by the number of eggs that survived through incubation. 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 date. When nestlings were fully feathered and disappeared between two successive visits, we assumed fledge date to be the midpoint between those visits. For some nests ($n = 10$), we observed all nestlings leaving the cavity simultaneously and assumed it to be the exact fledging date. We defined nest productivity as the number of fledglings produced per nesting attempt. We estimated breeding cycle duration as the days elapsed between laying of the first egg and fledging date. When nestlings were > 15 days, they generally observed nest surroundings from the cavity opening (A. Jauregui, *personal observation*). Hence, we attempted to minimize premature fledging risk by observing the cavity opening from a 5-10 m distance with binoculars.

Analysis

We assessed whether features at different spatial scales were related to nest survival and productivity using generalized linear models (GLMs). For nest survival, we estimated daily nest survival rate (DSR) using the logistic-exposure model (Schaffer 2004). For this model, the observation unit is the exposure period (time interval the nest was exposed expressed in days) between visits and the response variable is coded as 1 = survived the interval and 0 = did not survive the interval. Nest survival models were mixed models that included nest identity as a random factor to account for different intervals belonging to the same nest. We modeled productivity using Poisson probability distribution family and a log link function. We evaluated the relative support for all models using Akaike's information criterion corrected for small samples (AIC_c), interpreted as lower AIC_c = higher support, and vice versa (Burnham and Anderson 2002). For both response variables (DSR and productivity), we first built a null model without covariates. We then built models including individual and combined effects of temporal variables to decide whether to include a temporal structure in the subsequent environment related models. Specifically, we evaluated nest survival variation as a function of date and nest age (including linear and quadratic trends) and productivity variation as a function of date. All temporal models for both response variables received less support than the null model (had higher AIC_c values). Hence, we considered temporal variables to have no important relationships with the response variables and did not include them in subsequent models. We then built a set of models including simple (i.e., one variable per model) effects of cavity, cavity tree, and landscape features and combinations of these. Four models included more than one variable: (1) an interaction landscape model "forest cover*edge," (2) an additive landscape model "forest cover+edge," (3) a local scale model "cavity diameter+height+volume+cavity-tree DBH," and (4) a global model. We addressed model selection uncertainty by averaging models gathering 0.99 Akaike weight (w) using the natural average method (see Grueber et al. 2011). All variables were centered and standardized before running analyses and no variable was correlated to another one ($r < 0.7$, $VIF < 2$). The cumulative probability that a nest survived the breeding cycle was calculated by raising the daily survival rate estimated from the null model to a power represented by nesting cycle duration (days elapsed between laying of the first egg and fledging; see Weiser 2021). All analyses were performed in software R (R Development Team 2022), using MASS (Venables and Ripley 2002), lme4 (Bates et al. 2015), MuMIn (Barton 2020), and ggplot2 (Wickham 2016) packages. Reported values are means \pm SE.

RESULTS

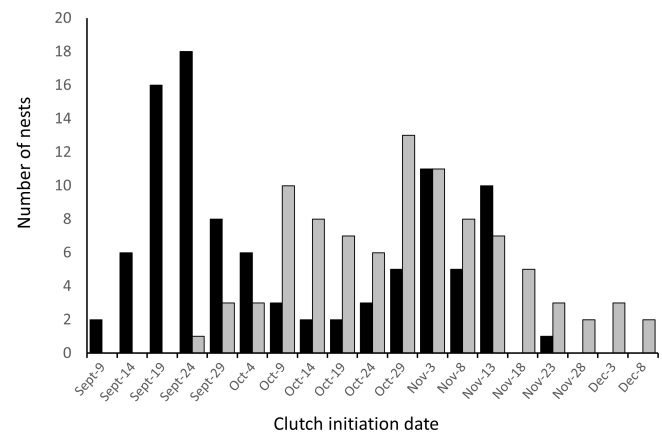
We found a total of 100 nesting attempts (39 in the 2020-2021 and 61 in the 2021-2022 breeding seasons), 13 of which were considered second broods. Four nests were found under construction, 28 during egg laying, 38 during incubation, and 30 during the nestling stage. Twenty-eight nesting attempts were in natural cavities, 70 were in woodpecker cavities, and 2 were in Rufous Hornero nests. Trees bearing cavities were 43 *Celtis tala*, 16 *Populus alba*, 6 *Eucalyptus* spp., 5 *Melia azedarach*, 1 *Casuarina* sp., 1 *Fraxinus* sp., 1 *Platanus acerifolia*, and 1 *Morus alba*. Cavity, cavity tree, and landscape 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).

Table 1. Measurements of cavities ($n = 85$), cavity trees, and the landscape surrounding them ($n = 74$) used by the European Starling (*Sturnus vulgaris*) to nest in forests of east-central Argentina between 2020 and 2022. Sample sizes differ because some cavities were in the same trees and were therefore surrounded by the same landscape.

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)
Diameter at breast height (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)

Fig. 1. Asynchrony of clutch initiation dates between the European Starling, *Sturnus vulgaris*, (black bars) and the Green-barred Woodpecker, *Colaptes melanochloros*, (grey bars) during two breeding seasons (2020-2021 and 2021-2022) in a south temperate forest of central-eastern Argentina. Bars represent the number of nests initiated during five-day intervals for which the underlying number is the median date of the interval.



Clutch size was 4.7 ± 0.1 eggs (range = 4-6 eggs, $n = 32$ nests), and median clutch size was 4 eggs. 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 hatchlings per nest (range = 3-5 hatchlings, $n = 30$ nests) and fledgling success 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 productivity was 2.7 ± 0.1 fledglings per nesting attempt (range = 1-5 fledglings, $n = 49$ nests). Productivity was not significantly different between first

and second broods ($t = 0.35$, $df = 28$, $P = 0.72$). None of the variables were significantly related to productivity because the null model was the most supported model (Table 2). The breeding cycle lasted 34.7 ± 0.2 days (range = 33-37 days, $n = 20$ nests).

Table 2. Top fitting models for daily survival rates (DSR) and productivity (number of fledglings) of starling nests in relation to nesting cavity, cavity-tree dimensions, and landscape variables in an Argentinian forest after monitoring nests between 2020 and 2022. We present models gathering 0.99 (DSR) and 0.90 (productivity) AICc weight (w_i). Df = degrees of freedom; logLik = log Likelihood; AICc = Akaike information criterion (corrected for small sample sizes); Δ = differences in AICc between models; and w_i = AICc weight. DBH = diameter at breast height, H = cavity height, V = cavity volume, D = cavity opening diameter, Edge = forest edge, FC = forest cover, and Global = including all the former variables.

Response	Variable	df	logLik	AIC _c	Δ	w_i
DSR	DBH	3	-70.8	147.7	0.0	0.67
	H+DBH+V+D	6	-68.6	149.9	2.2	0.23
	Global	8	-68.7	152.3	4.5	0.07
	Edge	3	-74.75	155.7	7.9	0.02
Productivity	Null	1	-57.8	117.8	0.0	0.28
	V	2	-57.6	119.7	1.9	0.11
	Date	2	-57.7	119.7	1.9	0.11
	D	2	-57.7	119.8	2.0	0.10
	Edge	2	-57.7	119.8	2.0	0.10
	FC	2	-57.7	119.8	2.0	0.10
	DBH	2	-57.8	120.0	2.2	0.09

There were 49 successful nesting attempts, 31 depredated (20 during incubation and 11 during nestling stages), 16 abandoned for unknown reasons (6 during incubation and 10 during the nestling stage), and in 4 cases we were not certain of nest fate. Apparent nest success was 49%. Time elapsed between 2 consecutive nesting attempts was 12.2 ± 0.4 days (range = 9-14 days, $n = 7$ nests) for failed nests and 11.8 ± 0.5 days (range = 7-14 days, $n = 13$ nests) for successful nests. Of these 13 successful first attempts, 7 breeding pairs produced a second successful brood. Daily survival rate was 0.973 ± 0.003 ($n = 392$ intervals), and mean exposure period (time between visits) was 5.7 ± 0.4 days (range = 1-10 days). The cumulative probability that an average nest survived was 38% (0.973^{35}). The most supported model included a negative influence of DBH on DSR (Tables 2 and 3 and Fig. 2). It was followed by the local scale model (including cavity and cavity-tree features effects) and the model including a simple edge effect (Table 2). The confidence intervals of the estimates of the latter two models included zero indicating only marginal relationships with DSR (Table 3), hence, there was only weak support for an effect of edge length on DSR. Contrary to our expectation, the model including an interaction between edge and forest cover was below the null model and had a ΔAIC_c of 12.1 with the top model, suggesting the interaction between forest cover and edge length had little support.

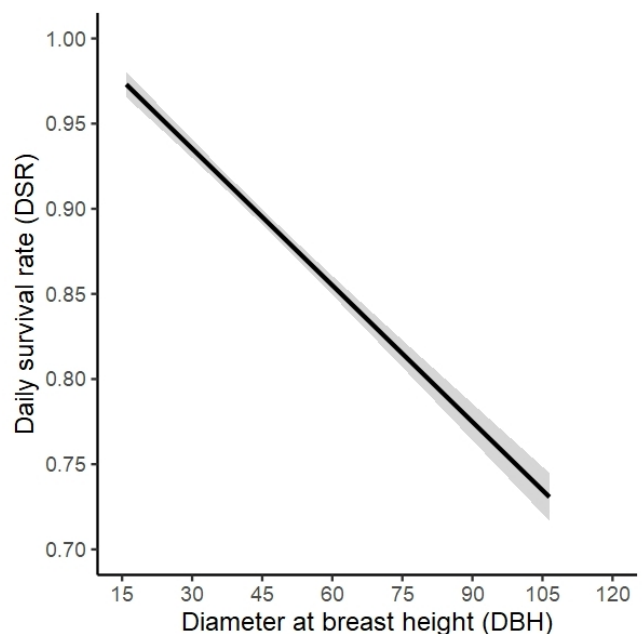
DISCUSSION

We found that nest survival of the starling was inversely related to DBH, which contradicted our predictions. This could be crucial information if starlings continue their expansion into northeast Argentina, a region inhabited by many threatened cavity-nesting

Table 3. Model averaged estimates indicate diameter at breast height (DBH) was the only variable importantly related to nest daily survival rates (DSR) for a European Starling (*Sturnus vulgaris*) population breeding in east-central Argentina between 2020 and 2022. We averaged the estimates of models gathering 0.99 w_i (Akaike weight) using the “natural average” method (see Grueber et al. 2011 for details). Estimates are accompanied by their adjusted standard errors (Adj SE), 95% confidence intervals (CIs), and relative importance. Diameter = cavity opening diameter.

Variable	Estimate	Adj SE	Lower CI	Upper CI	Importance
Intercept	3.51	0.20	3.12	3.90	-
DBH	-0.70	0.23	-1.16	-0.25	0.99
Diameter	0.43	0.23	-0.01	0.88	0.23
Cavity height	0.06	0.21	-0.36	0.48	0.30
Cavity volume	-0.10	0.20	-0.50	0.31	0.30
Forest cover	-0.04	0.39	-0.81	0.73	0.07
Edge	-0.31	0.38	-1.05	0.44	0.08

Fig. 2. European Starling (*Sturnus vulgaris*) nest daily survival rate has an inverse relationship with diameter at breast height (DBH; model built using the logistic-exposure method of Schaffer 2004) on a population breeding in central-eastern Argentina between 2020 and 2022. Black solid line represents the average relationship and grey areas surrounding it are the standard error.



species (Cockle et al. 2015, eBird 2022). In this region, human timber logging is reducing forests containing large mature trees, increasing the presence of logged forests with openings (Cockle et al. 2015). These modified forests could potentially increase the breeding success of the starling. However, whether this pattern applies to starling populations in the northern limits of its

expanding range should be further studied and understanding the causes of such relationship would be helpful to determine how this invasive species is benefited by smaller trees. Regardless of nest survival patterns, 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 reported for its original distribution area (Korpimäki 1978, Mazgajski 2007), this breeding success rate is relatively 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* (Llambías and Fernández 2008), and double the ~19% of *Agelaioides badius* (de Mársico et al. 2010). This success rate resembles the ~41% of *Colaptes campestris* and *Colaptes melanochloros* (Cockle et al. 2015, Jauregui 2020), two native woodpeckers, though starling productivity (2.7) was slightly higher (*C. campestris* = 2.2 fledglings, *C. melanochloros* = 2.5 fledglings; Jauregui 2020). Moreover, there were seven breeding pairs that we assume produced fledglings twice in the same breeding season, a situation not found in woodpeckers (Jauregui 2020). Therefore, our results suggest productivity and estimated nest survival are relatively higher than that of native woodpeckers and secondary cavity-nesting species, respectively. To fully understand whether starlings are recruiting new individuals at a higher rate than native species, year-round mortality rates would be needed. Regardless, these results, after a relatively recent invasion, suggest that the population will continue to grow and expand.

We were surprised by the negative relationship between cavity tree DBH and nest survival because it 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 accustomed to them, as 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 (A. Jauregui, *personal observation*). Nevertheless, during data exploration, we were not able to find a significant relationship between cavity-tree species and nest fate. Larger trees may support deeper cavities, which could be related to either higher nest survival (Cockle et al. 2015) or may impact cavity temperature (Jauregui et al. 2022). However, there was no relationship between nest survival or productivity with cavity volume, hence, depth. Whichever is the case, because of 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 to clarify this pattern.

Contrary to our predictions, edge and forest cover had poor relationships with DSR and productivity. Starlings frequently inhabit semi-open forests mixed with grassland openings (Wiebe 2004). However, habitats with the conditions preferred by species may not always translate to high nest success (Zhu et al. 2012). For instance, it has been proposed that forest edges may be associated with high predator abundance and activity (Shew et

al. 2019). Hence, despite the possible benefits of nesting in forests with larger amounts of foraging habitat available (e.g., short distances to food sources), there may also be costs, such as high predation rates (Shew et al. 2019). In fact, the inverse relationship of edge with DSR would support this idea, but we found very little support for this hypothesis to make such an inference. Moreover, as forest cover and edge were not related to productivity, this habitat may provide enough food resources (assumed to limit productivity) regardless of landscape configuration. A specific assessment of starling feeding habits in these forests would help with this topic. We believed human-related forest fragmentation (which modified these forests' natural structure) would translate into differences across nests, which we could not find. For example, it is possible that because these forests have a natural semi-open nature, we could not capture enough variation in the landscape to detect such differences. Also, because we found one third of the nests during the nestling stage, there is a chance that patterns are biased by nest stage at encounter. However, nest survival estimates theoretically are not biased by nest age at finding because the logistic-exposure model corrects for nests not found (Schaffer 2004 and articles there cited). Furthermore, because two-thirds of nests were found during egg laying and incubation (of which 20 were predated during this stage), this bias seems unlikely. Despite these possibilities, our findings suggests that none of the measured landscape variables are related to the breeding success of this starling population.

The starling clutch initiation peaked in September, indicating a synchronous start of nest initiation within the population as previously reported (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, though there is an important breeding overlap between October and December (Llambías and Fernández 2008, de la Peña 2016, Jauregui et al. 2019). An early start in the breeding season could favor starling breeding success by avoiding competition with native species for cavity use. Moreover, the time elapsed between first and second broods was relatively short (~12 days), even for successful nests for which adults must attend to recent fledglings. Consequently, given there are several species using cavities in the area, starlings may have an advantage in successfully occupying one because they start earlier and have relatively short re-nesting periods. Furthermore, starlings may also overcome cavity availability limitation because they have proven to be considerably successful cavity usurpers through aggressive behaviors (Frei et al. 2015 and Jauregui et al. 2021 and articles there cited). Starlings usurping cavities of native species would delay nest initiation dates of the latter, which could decrease their nesting success and re-nesting probability (Wiebe 2003). Nest success of native birds is considerably reduced by the end of the season at these latitudes, probably due to an increase in predator activity (Segura and Reboreda 2012, Jauregui 2020) and higher ectoparasite incidence (Segura and Palacio 2021).

Among global biological invasions, South American ones are known to cause severe economic impacts (Heringer et al. 2021), and they have been considerably less studied than their northern counterparts (Darrigran et al. 2020, Heringer et al. 2021). High starling breeding success, relative to that of native species, may not only pose a threat to the native fauna but is also likely to cause severe economic problems as populations of the species feed on

crops (Bozzo et al. 2021). In fact, there are already records of starlings attacking crops (Ibañez et al. 2016), and recent estimations of annual losses in the country have reached 130 million U.S. dollars (MAyDS 2022). Our findings constitute the first record of breeding success (and its relationship with environmental features), habitat use, and the basic nesting biology data from an invasive starling population in Argentina. Results suggest that the exponential growth and expansion of the starling population in South America (Zufiaurre et al. 2016, Codesido and Drozd 2021) is likely to continue. Such contributions are crucial as a baseline to work on species control (Rodríguez 2001), and information reported regarding starling nest-site characteristics and their relationship with breeding success 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). However, further studies are needed to fully understand the impacts and status of starling populations on the continent. If starlings are shown to compete directly with Neotropical native species they encounter (Ibañez et al. 2017, Jauregui et al. 2021), more direct control measures may be needed.

Author Contributions:

Adrián Jauregui and Luciano Noel Segura conceived and designed the study. Data collection and analysis were performed by Adrián Jauregui, Martín Alejandro Colombo, and Paula Agustina Gerstmayr. Luciano Noel Segura provided funding for the study. The first draft of the manuscript was written by Adrián Jauregui and Luciano Noel Segura, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Acknowledgments:

We thank M. L. Shaw who let us undertake the study in Luis Chico. We also thank V. Monges, L. Demarchi, L. González-García, A. Mellum, and E. Gonzalez for the help during field work. We kindly thank K. Wiebe, an anonymous reviewer, and the subject editor for their comments, which substantially improved our manuscript. We thank T. Lansley and K. Depot for their comments in a previous version of the manuscript. This paper is the Scientific Contribution N° 1230 of the Institute of Limnology “Dr. Raúl A. Ringuelet” (ILPLA, CCT-La Plata CONICET, UNLP). This study was conducted with research permits from the regional nature conservation authority (Res. 003/16; OPDS #17717, Dirección de Áreas Naturales Protegidas, Buenos Aires province, Argentina) and complies with the current laws of the country in which they were performed. Partial financial support was received from ‘Proyecto Acreditado de Incentivos, Universidad Nacional de La Plata’ under grant number 11/N930.

LITERATURE CITED

Arturi, M. F., and J. F. Goya. 2004. Estructura, dinámica y manejo de los talaes del NE de Buenos Aires. Pages 1-23 in M. F. Arturi, J. L. Frangi, and J. F. Goya, editors. *Ecología y manejo de los bosques de Argentina*. Edulp, La Plata, Buenos Aires, Argentina.

Barton, K. 2020. MuMIn: multi-model inference. R package version 1.43.17. R Foundation for Statistical Computing, Austria, Vienna. <https://CRAN.R-project.org/package=MuMIn>

Bates, D., M. Mäechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1):1-48. <https://doi.org/10.18637/jss.v067.i01>

Berl, J. L., J. W. Edwards, J. S. Bolsinger, and T. E. Katzner. 2014. Survival of Red-headed Woodpeckers’ (*Melanerpes erythrocephalus*) nests in northern New York. *Wilson Journal of Ornithology* 126 (4):700-707. <https://doi.org/10.1676/14-009.1>

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26(7):333-339. <https://doi.org/10.1016/j.tree.2011.03.023>

Bozzo, F., S. Tarricone, A. Petrontino, P. Cagnetta, G. Maringelli, G. La Gioia, V. Fucilli, and M. Ragni. 2021. Quantification of the starling population, estimation and mapping of the damage to olive crops in the Apulia region. *Animals* 11(4):1119. <https://doi.org/10.3390/ani11041119>

Bruun, M., and H. G. Smith. 2003. Landscape composition affects habitat use and foraging flight distances in breeding European Starlings (*Sturnus vulgaris*). *Biological Conservation* 114(2):179-187. [https://doi.org/10.1016/S0006-3207\(03\)00021-1](https://doi.org/10.1016/S0006-3207(03)00021-1)

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, New York, New York, USA. <https://doi.org/10.1007/b97636>

Cabe, P. R. 2020. European Starling (*Sturnus vulgaris*). Version 1.0. In S. M. Billerman, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.eursta.01>

Codesido, M., and A. Drozd. 2021. Alien birds in Argentina: pathways, characteristics and ecological roles. *Biological Invasions* 23:1329-1338. <https://doi.org/10.1007/s10530-020-02444-w>

Cockle, K. L., A. Bodrati, M. Lammertink, and K. Martin. 2015. Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic forest. *Biological Conservation* 184:193-200. <https://doi.org/10.1016/j.biocon.2015.01.026>

Darrigran, G., I. Agudo-Padrón, P. Baez, C. Belz, F. Cardoso, A. Carranza, G. Collado, M. Correo, M. G. Cuzzo, A. Fabres, D. E. Gutiérrez Gregoric, S. Letelier, S. Ludwig, M. C. Mansur, G. Pastorino, P. Penchaszadeh, C. Peralta, A. Rebolledo, A. Rumi, S. Santos, S. Thiengo, T. Vidigal, and C. Damborenea. 2020. Non-native mollusks throughout South America: emergent patterns in an understudied continent. *Biological Invasions* 22:853-871. <https://doi.org/10.1007/s10530-019-02178-4>

de la Peña, M. R. 2016. Aves Argentinas: descripción, comportamiento, reproducción y distribución. Trogonidae a Furnariidae. Comunicaciones Museo Provincial Ciencias Naturales Florentino Ameghino, Santa Fe, Argentina. http://www.coarecs.com.ar/folletos/aa_dlp3.pdf

- de Mársico, M. C., B. Mahler, and J. C. Reboreda. 2010. Reproductive success and nestling growth of the Baywing parasitized by Screaming and Shiny cowbirds. *Wilson Journal of Ornithology* 122(3):417-431. <https://doi.org/10.1676/09-140.1>
- eBird. 2022. An online database of bird distribution and abundance. eBird, Cornell Lab of Ornithology, Ithaca, New York, USA. <https://www.ebird.org/>
- Feare, C. J., P. Douville de Franssu, and S. J. Peris. 1992. The starling in Europe: multiple approaches to a problem species. Pages 83-88 in J. E. Borreco and R. E. Marsh, editors. *Proceedings of the Vertebrate Pest Conference 15*, University of California, Davis, USA. <https://escholarship.org/uc/item/3n3895n3>
- Flux, J. E. C., and M. M. Flux. 1981. Population dynamics and age structure of starlings in New Zealand. *New Zealand Journal of Ecology* 4:65-72.
- Frei, B., J. J. Nocera, and J. W. Fyles. 2015. Interspecific competition and nest survival of the threatened Red-headed Woodpecker (*Colaptes melanochloros*). *Journal of Ornithology* 156:743-753. <https://doi.org/10.1007/s10336-015-1177-6>
- Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24(4):699-711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Heger, T., and L. Trepl. 2003. Predicting biological invasions. *Biological Invasions* 5:313-321. <https://doi.org/10.1023/B:BINV.000005568.44154.12>
- Heringer, G., E. Angulo, L. Ballesteros-Mejia, C. Capinha, F. Courchamp, C. Diagne, V. G. Duboscq-Carra, M. A. Nuñez, and R. Dudeque Zenni. 2021. The economic costs of biological invasions in Central and South America: a first regional assessment. *NeoBiota* 67:401-426. <https://doi.org/10.3897/neobiota.67.59193>
- Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96(1):73-77. <https://doi.org/10.1093/auk/96.1.73>
- Ibañez, L. M. 2015. Invasión del Estornino Pinto *Sturnus vulgaris* en el Noreste de la provincia de Buenos Aires: análisis de la competencia con aves nativas y potencialidad como transmisor de parásitos. Dissertation. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina. <http://sedici.unlp.edu.ar/handle/10915/45048>
- Ibañez, L. M., F. Andreucci, and D. Montalti. 2016. First record of crop damage on fruit trees by the European Starling (*Sturnus vulgaris*) (Passeriformes: Sturnidae) in Argentina. *Acta Zoologica Lilloana* 60(2):177-180.
- Ibañez, L. M., J. M. Girini, F. X. Palacio, V. D. Fiorini, and D. Montalti. 2017. Interacciones entre el Estornino Pinto (*Sturnus vulgaris*) y aves nativas de Argentina por el uso de cavidades. *Revista Mexicana de Biodiversidad* 88(2):477-479. <https://doi.org/10.1016/j.rmb.2017.03.009>
- InBiAr. 2022 Government data base. Base de datos sobre invasiones biológicas en Argentina. GEKKO, Grupo de Estudios en Conservación y Manejo, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, Bahía Blanca, Argentina. <http://www.inbiar.uns.edu.ar/base-dados-nacional>
- Jauregui, A. 2020. Selección de sitios de nidificación y efecto del hábitat en el éxito reproductivo de *Colaptes campestris* (*Carpintero campestre*) y *Colaptes melanochloros* (*Carpintero real*) (Aves: Picidae) en talaes bonaerenses. Dissertation. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina. <http://sedici.unlp.edu.ar/handle/10915/90390>
- Jauregui, A., E. Gonzalez, and L. N. Segura. 2019. Nesting biology of the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) in a southern temperate forest of central-east Argentina. *Studies on Neotropical Fauna and Environment* 54(2):114-120. <https://doi.org/10.1080/01650521.2019.1590968>
- Jauregui A., E. Gonzalez, and L. N. Segura. 2021. Impacts of the invasive European Starling (*Sturnus vulgaris*) on two neotropical woodpecker species: agonistic responses and reproductive interactions. *Emu - Austral Ornithology* 121(3):223-230. <https://doi.org/10.1080/01584197.2021.1920841>
- Jauregui A., E. Gonzalez, and L. N. Segura. 2022. Multi-scale nest survival analysis suggests new cavities improve nest success for the Green-barred Woodpecker, but not the Campo Flicker, in a threatened woodland of Argentina. *Ornithological Applications* 124(4):1-13. <https://doi.org/10.1093/ornithapp/duac039>
- Kerpez, T. A., and N. A. Smith. 1990. Competition between European Starlings (*Sturnus vulgaris*) and native woodpeckers for nest cavities in saguaros. *Auk* 107(2):367-375. <https://doi.org/10.2307/4087621>
- Kessel, B. 1957. A study of the breeding biology of the European Starling (*Sturnus vulgaris* L.) in North America. *American Midland Naturalist Journal* 58(2):257-331. <https://doi.org/10.2307/2422615>
- Koenig, W. 2002. European Starlings (*Sturnus vulgaris*) and their effect on native cavity-nesting birds. *Conservation Biology* 17(4):1134-1140. <https://doi.org/10.1046/j.1523-1739.2003.02262.x>
- Korpimäki, E. 1978. Breeding biology of the Starling *Sturnus vulgaris* in western Finland. *Ornis Fennica* 55:93-104. https://lintulehti.birdlife.fi:8443/pdf/artikkelit/914/tiedosto/of_55_93-104_artikkelit_914.pdf
- Lafleur, N. E., M. A. Rubega, and C. S. Elphick. 2007. Invasive fruits, novel foods, and choice: an investigation of European Starling and American Robin frugivory. *Wilson Journal of Ornithology* 119(3):429-438. <https://doi.org/10.1676/05-115.1>
- Levine, J. M. 2008. Biological invasions. *Current Biology* 18(2):57-60. <https://doi.org/10.1016/j.cub.2007.11.030>
- Linz, G. M., H. J. Homan, S. M. Gaulker, L. B. Penry, and W. J. Bleier. 2007. European Starlings: a review of an invasive species with far-reaching impacts. *Managing vertebrate invasive species: proceedings of an international symposium*. National Wildlife Research Center, Fort Collins, Colorado, USA. <https://digitalcommons.unl.edu/nwrcinvasive/24>

- Llambías, P. E., and G. J. Fernández. 2008. Effects of nestboxes on the breeding biology of Southern House Wrens *Troglodytes aedon bonariae* in the southern temperate zone. *Ibis* 151 (1):113-121. <https://doi.org/10.1111/j.1474-919X.2008.00868.x>
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), University of Auckland, Auckland, New Zealand. <https://portals.iucn.org/library/sites/library/files/documents/2000-126.pdf>
- MAyDS. 2022. Management program, Ministerio de Ambiente y Desarrollo Sostenible de la Nación, Buenos Aires, Argentina. <https://www.argentina.gob.ar/ambiente/biodiversidad/exoticas-invasoras/estrategia>
- Mazgajski, T. D. 2003. Nesting interaction between woodpeckers and starlings - delayed commensalism, competition for nest sites or cavity kleptoparasitism? Pages 133-138 in P. Pechacek and W. D'Oleire-Oltmanns, editors. International Woodpecker Symposium. Proceedings. Forschungsbericht 48, Nationalparkverwaltung Berchtesgaden, Germany.
- Mazgajski, T. D. 2007. Effect of old nest material in nestboxes on ectoparasite abundance and reproductive output in the European Starling (*Sturnus vulgaris* L.). *Polish Journal of Ecology* 55:377-385. <https://www.infona.pl/resource/bwmeta1.element.baztech-article-BGPK-1772-6518>
- Nyrienda, V. R., F. C. Chewe, E. Chisha-kasumu, P. A. Lindsey, and K. C. Mine. 2016. Nest sites selection by sympatric cavity-nesting birds in miombo woodlands. *Koedoe* 58(1):a1359. <http://dx.doi.org/10.4102/koedoe.v58i1.1359>
- Ojanen, M., M. Orell, and J. Hirvelä. 1979. The breeding biology of the Starling *Sturnus vulgaris* in northern Finland. *Ecography* 2(2):81-87. <https://doi.org/10.1111/j.1600-0587.1979.tb00685.x>
- Ojeda, V., M. L. Chazarreta, J. F. Masello, F. Buglione-Rodríguez, and M. Failla. 2022. European Starlings (*Sturnus vulgaris*) expand into Patagonia. Time for action. *Global Ecology and Conservation* 39:e02295. <https://doi.org/10.1016/j.gecco.2022.e02295>
- Peris, S. P. A., G. E. Soave, A. R. Camperi, C. A. Darrieu, and R. M. Aramburu. 2005. Range expansion of the European Starling *Sturnus vulgaris* in Argentina. *Ardeola* 52(2):359-364. <https://www.ardeola.org/en/volumes/522/articles/359-364/>
- Quantum Geographic Information System (QGIS) Development Team. 2018. QGIS. Open Source Geospatial Foundation Project, Beaverton, Oregon, USA. <http://qgis.osgeo.org/>
- R Development Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.Rproject.org/>
- Rebolo Ifran, N., and V. D. Fiorini. 2010. European Starling (*Sturnus vulgaris*): population density and interactions with native species in Buenos Aires urban parks. *Ornitologia Neotropical* 21 (4):507-518. <https://sora.unm.edu/sites/default/files/ON%201%20%284%29%20507-518.pdf>
- Rodríguez, J. P. 2001. La amenaza de las especies exóticas para la conservación de la biodiversidad Suramericana. *Interciencia* 26 (10):479-483. <https://www.redalyc.org/pdf/339/33906110.pdf>
- Royall Jr., W. C. 1966. Breeding of the starling in Central Arizona. *Condor* 68(2):196-205. <https://doi.org/10.2307/1365718>
- Schaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121(2):526-540. <https://academic.oup.com/auk/article/121/2/526/5562433>
- Segura, L. N., E. Gonzalez, F. M. Harguindeguy, M. A. Colombo, and A. Jauregui. 2019. Food delivery rates increased with forest canopy cover and nestling growth improved with arachnids in the Masked Gnatcatcher *Poliptila dumicola*. *Acta Ornithologica* 54 (2):233-241. <https://doi.org/10.3161/00016454AO2019.54.2.009>
- Segura, L. N., and F. X. Palacio. 2021. Quantifying the relative importance of direct and indirect effects influencing bird nestling growth. *Integrative Zoology* 17(3):408-419. <https://doi.org/10.1111/1749-4877.12544>
- Segura, L. N., and J. C. Reboresda. 2012. Nest survival rates of Red-crested Cardinals increase with nest age in south-temperate forests of Argentina. *Journal of Field Ornithology* 83(4):343-350. <https://doi.org/10.1111/j.1557-9263.2012.00384.x>
- Shew, J. J., C. K. Nielsen, and D. W. Sparling. 2019. Finer-scale habitat predicts nest survival in grassland birds more than management and landscape: a multi-scale perspective. *Journal of Applied Ecology* 56(4):929-945. <https://doi.org/10.1111/1365-2664.13317>
- Silva, F. C., J. Motta da Pinto, A. Mädder, and V. A. Teixeira de Souza. 2017. First records of European Starling *Sturnus vulgaris* in Brazil. *Revista Brasileira de Ornitologia* 25:297-298. <https://doi.org/10.1007/BF03544409>
- Smith, H. G., A. Ryegård, and S. Svensson. 2012. Is the large-scale decline of the starling related to local changes in demography? *Ecography* 35:741-748. <https://doi.org/10.1111/j.1600-0587.2011.06310.x>
- Venables, W., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.
- Weiser, E. L. 2021. Fully accounting for nest age reduces bias when quantifying nest survival. *Ornithological Applications* 123 (3):duab030. <https://doi.org/10.1093/ornithapp/duab030>
- Wickham, H. 2016. Ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, New York, USA.
- Wiebe, K. L. 2003. Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers. *Oikos* 100(2):291-298. <https://doi.org/10.1034/j.1600-0706.2003.12046.x>
- Wiebe, K. L. 2004. Innate and learned components of defence by flickers against a novel nest competitor, the European Starling. *Ethology* 110(10):779-791. <https://doi.org/10.1111/j.1439-0310.2004.01016.x>
- Wiebe, K. L., W. D. Koenig, and K. Martin. 2007. Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici* 44(3):209-217. <https://www.>

[semanticscholar.org/paper/Costs-and-benefits-of-nest-reuse-versus-excavation-Wiebe-Koenig/cf621c3fa884d20b219c39d3927495123bd981b2](https://www.semanticscholar.org/paper/Costs-and-benefits-of-nest-reuse-versus-excavation-Wiebe-Koenig/cf621c3fa884d20b219c39d3927495123bd981b2)

Wiebe, K. L., and T. L. Swift. 2003. Clutch size relative to cavity size in Northern Flickers. *Journal of Avian Biology* 32(2):167-173. <https://doi.org/10.1034/j.1600-048X.2001.320210.x>

Williams, D. R., M. F. Child, L. V. Dicks, N. Ockendon, R. G. Pople, D. A. Showler, J. Walsh, E. K. H. J. zu Ermgassen, and W. J. Sutherland. 2019. Bird conservation. Pages 141-290 in W. J. Sutherland, L. V. Dicks, N. Ockendon, S. O. Petrovan, and R. K. Smith, editors. *What works in conservation 2019*. Open Book Publishers, Cambridge, UK.

Zhu, X., D. S. Srivastava, J. N. M. Smith, and K. Martin. 2012. Habitat selection and reproductive success of Lewis's Woodpecker (*Melanerpes lewis*) at its northern limit. *PLoS ONE* 7(9):e44346. <https://doi.org/10.1371/journal.pone.0044346>

Zufiaurre, E., A. Abba, D. Bilenca, and M. Codesido. 2016. Role of landscape elements on recent distributional expansion of European Starlings (*Sturnus vulgaris*) in agroecosystems of the Pampas, Argentina. *Wilson Journal of Ornithology* 128 (2):306-313. <https://doi.org/10.1676/wils-128-02-306-313.1>

Editor-in-Chief: Alexander L. Bond
Subject Editor: Greg Mitchell



Sponsored by the Society of
Canadian Ornithologists and
Birds Canada

Parrainée par la Société des
ornithologistes du Canada et
Oiseaux Canada

