

Rewinding the invasion history of monk parakeets in Barcelona city: 1976-2022

N. A. Borray-Escalante^{1,2}, Z. Nuñez-Tobajas², X. Batllori², D. Santos³, J. Clavell³, J. Domènech², L. Arroyo², F. Uribe², R. Rodríguez-Pastor^{2,4,5}, J. Pascual², J. G. Carrillo-Ortiz², B. Molina⁷, J. C. del Moral⁷, T. Montalvo⁶, L. Cardador¹, B. Hatchwell⁸, J. C. Senar²

Author affiliations:

- ¹ University of Barcelona, Spain
² Museu de Ciències Naturals de Barcelona, Spain
³ Grupo de Aves Exóticas, SEO/BirdLife, Spain
⁴ Veterinary Faculty, University of Zaragoza, Spain
⁵ IA2, CITA, University of Zaragoza, Spain
⁶ Agencia de Salud Pública de Barcelona, Spain
⁷ SEO/BirdLife, Madrid, Spain
⁸ University of Sheffield

Corresponding author:

NA Borray-Escalante
nborrayescalante@gmail.com

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Abstract

Rewinding the invasion history of monk parakeets in Barcelona city: 1976-2022. Predicting the future abundance and distribution of introduced alien species is crucial to mitigate their impact on ecosystems, but this has been shown to be highly challenging. A good approach to obtain crucial clues to the root causes behind dynamic changes over time and space of invasive species is historical re-surveys. Barcelona holds one of the largest densities in Europe of monk parakeets *Myiopsitta monachus*, a highly successful invasive avian alien species. In this study, we evaluate population size, population growth rates and range expansion across the city, performing periodic nest and chamber counts from detection of the first nest in 1976 to 2022. Population estimates of monk parakeets during the study period showed a steady increase, reaching $6,444 \pm 449$ individuals in 2022. The population exhibited exponential growth with a mean population growth rate of $r = 0.19$ per year, which means a population doubling time of 3.7 years. Furthermore, two phases were evident: the first from 1976 to 1994 with a growth rate of 0.37 and a population doubling time of 1.9 years; and the second from 1999 to 2022 with a growth rate of 0.08 and a time to double the population of nine years. Moreover, we document the expansion of the range during our study through the colonisation of new areas, which fitted to a diffusion model for the whole period. Currently, the growth rate of the invasive monk parakeet population does not appear to be limited by resources, nest availability, disease, or predators and we expect them to continue increasing and expanding their range if no control measures are taken.

Key words: Monk parakeets, Population size, Population growth, Exponential growth, Range expansion, Exotic species

Resumen

Rebobinando la invasión de las cotorras argentinas en la ciudad de Barcelona: 1976-2022. Predecir la abundancia y distribución futuras de especies exóticas introducidas es crucial para mitigar su impacto en los ecosistemas, pero es una tarea ardua. Una buena manera de obtener pistas cruciales sobre las causas fundamentales de los cambios dinámicos en el tiempo y el espacio de las especies invasoras son los nuevos estudios históricos. Barcelona tiene una de las mayores densidades de Europa de cotorra argentina, *Myiopsitta monachus*, una especie de ave exótica invasora de gran éxito. En este estudio, evaluamos el tamaño de la población, la tasa de crecimiento demográfico y la expansión del área de distribución en toda la ciudad, realizando conteos periódicos de nidos y cámaras desde que se detectó el primer nido en 1976 hasta 2022. Las estimaciones de la población de cotorra argentina durante el período de estudio mostraron un aumento constante hasta llegar a 6.444 ± 449 individuos en 2022. La población creció exponencialmente con una tasa media de crecimiento demográfico de $r = 0,19$ por año, lo que significa que el tiempo de duplicación poblacional es de 3,7 años. Además, se podían diferenciar dos fases: la primera de 1976 a 1994, con una tasa de crecimiento de 0,37 y un tiempo de duplicación de la población de 1,9 años, y la segunda de 1999 a 2022, con una tasa

de crecimiento de 0,08 y un tiempo para duplicar la población de nueve años. Además, documentamos la expansión del área de distribución durante nuestro estudio mediante la colonización de nuevas áreas, que se ajustó a un modelo de difusión durante todo el período. Actualmente, la tasa de crecimiento de la población de cotorra argentina no parece estar limitada por los recursos, la disponibilidad de nidos, las enfermedades ni los depredadores y prevemos que la especie continúe aumentando y ampliando su área de distribución si no se toman medidas de control.

Palabras clave: Cotorra argentina, Tamaño poblacional, Crecimiento poblacional, Crecimiento exponencial, Expansión del área de distribución, Especie exótica

Introduction

Biological invasions by alien species can have significant effects on native biota and are widely considered one of the most serious threats to biodiversity at the global level (Swanson 1995, Simberloff et al 2013, Bellard et al 2014, Hernández-Brito et al 2014). Indeed, aliens have been associated with almost one-third of known global species extinctions since 1500, more than any other driver (Blackburn et al 2019). Alien birds alone have been shown to have substantial negative impacts on native species through such diverse mechanisms such as hybridization, predation, competition and spread of disease (Blackburn et al 2009, Evans et al 2016). Various modes of introduction of non-native species have been identified (Ruiz and Carlton 2003), and most introduced species essentially start with small populations (Sakai et al 2001). Two main processes characterise invasive species: exponential population growth and range expansion, and they are often preceded by a lag-phase, that is, a period of slow population growth during which organisms adapt to the new habitat followed by a marked increase in the growth rate (Sakai et al 2001, Crooks 2005, Aikio et al 2010). Understanding the population growth and range expansion of invasive species is essential in order to cope with the mechanisms that lead some species to be invasive and to help develop management strategies (Sakai et al 2001, Byers et al 2002, Garnas et al 2016, Menke and Holway 2020).

Valuable insights into the underlying mechanisms of long-term shifts in introduced species populations can be gleaned from historical resurveys, which document spatial and temporal patterns in population size and distribution with new data and their comparisons with old data (Estoup and Guillemaud 2010, Fidino et al 2022). While predicting the future abundance and distribution of introduced species remains challenging, these extended surveys offer crucial clues to the root causes behind dynamic changes over time (Menke and Holway 2020). However, long-term studies of species introductions are, in general, rare (Strayer 2012), and data are often sparse and incomplete, especially during the first invasive stages (Estoup and Guillemaud 2010). Notable exceptions may be, for instance, the spread of starlings *Sturnus*

vulgaris (Wing 1943), house sparrows *Passer domesticus* (Wing 1943, Peña-Peniche et al 2021), house finches *Haemorhous mexicanus* (Veit and Lewis 1996), argentine ants *Linepithema humile* and collared doves *Streptopelia decaocto* (Bled et al 2010) in North America, Asian hornets *Vespa velutina nigrithorax* (Robinet et al 2017) in Europe, and cane toads *Rhinella marina* (Macgregor et al 2021) in Australia.

The monk parakeet *Myiopsitta monachus*, native to South America, is considered the most invasive parrot species, having invaded numerous areas across North America, Europe and Asia with great success (Postigo et al 2019). With the rise of economic prosperity in the 1960s, these parrots became popular pets, and thousands of birds were exported around the world (Souviron-Priego et al 2018, Cardador et al 2021). This was facilitated by the fact that it caused economic damage in its countries of origin, which allowed unlimited exploitation (Bucher 1992, Minor et al 2012). In the 1970s, the wild bird trade was huge and in the 1990s, international bird trade was estimated at 5 million birds per year (FAO 2011). Furthermore, as monk parakeets were very abundant, the sale price was low, which further increased its trade (Bull 1973). As a consequence, millions of wild monk parakeets were captured and transported from their native area to homes around the world (Edelaar et al 2015, Cardador et al 2021). Accidental escapes or local intentional releases then resulted in the establishment of new self-sustaining wild populations. These populations have exhibited rapid growth since 1970, both in Europe and America (van Bael and Pruett-Jones 1996, Avery et al 2002, Domènech et al 2003, Pruett-Jones et al 2005, Postigo et al 2019, Pruett-Jones 2021, Senar et al 2021, Senar and Carrete 2022, Huerta-Sánchez et al 2023). Consequently, the negative impacts related to these birds have also increased.

In Barcelona the first monk parakeets were detected at the start of the 60s, and the first nest was detected in 1976 (Ferrer 2016). In fact, Barcelona was the first city in Europe where a viable population of the species was detected (Senar and Carrillo-Ortiz 2020). Since then, the population has been growing rapidly, both in number of individuals and in their range, and likewise, the damage caused has been increasing (Senar et al 2016). Such damage includes

direct effects in many ways, such as on the infrastructure of light poles and other elevated lighting, on the vegetation, since due to the large size and weight of the nests the branches on which they rest can break (Senar 2021), on public health due to the danger of disease transmission, such as Psittacosis or Newcastle disease (Senar 2021, Blanco-González et al 2023), and on agriculture, where losses of up to 37% have been recorded in crops such as tomato, corn, plum, pear, persimmon and quince (in the metropolitan area) (Senar et al 2016), reaffirming the importance of population control (Senar 2021). Studying the population growth and range expansion of monk parakeets is crucial because knowledge of the number of individuals and the invaded areas can be used to construct biologically meaningful population models to direct management decisions. In this study, we aimed to assess the invasion history of the monk parakeet in the city of Barcelona, providing detailed information based on historical records, including population estimates, population growth rates and range expansion. We also address the possible factors that may have contributed to the successful establishment of monk parakeets in Barcelona city.

Materials and methods

This study was conducted in Barcelona city, Spain, on the northeast coast of the Iberian Peninsula. Barcelona has an area of 102.16 km², 72.34% is built. We incorporated data collected throughout the project into our database, creating a comprehensive historical record of the invasion process in the city of Barcelona.

Data were used from published and unpublished reports of the various nests in the city of Barcelona dating from 1976 to 2022. For the oldest censuses (70s, 80s and 90s) the nests were not georeferenced, so the original maps have been used (Batllori and Nos 1985, Clavell et al 1991, Román-Muñoz and Ferrer 1997, Sol et al 1997) and each nest has been georeferenced. For the most recent censuses (Domènech et al 2003, Rodríguez-Pastor et al 2012, Pascual et al 2015), data from already georeferenced nests were used. With all these data, new maps were created in QGIS (version 3.22) to visualise the population growth and occupation of the city area from 1981 to 2022 (projection: UTM 31N). All the censuses were conducted with a similar sampling effort both over time and across the different areas of Barcelona, since all the censuses were conducted under the direction of the Museu de Ciències Naturals de Barcelona.

As the nests of this species contain several chambers, which are used throughout the year for breeding and roosting, we based the study on the enumeration of nests and chambers over the years. This method is more reliable when estimating the population size of this species than the direct count of individual, since its great mobility means that the same individuals can easily be counted more than once, generating a population overestimation (Faus and Senar 2010, Senar and Carrillo-Ortiz 2007). Hence, we used the total number of chambers found to make an indirect estimate of the population size. Since a chamber may

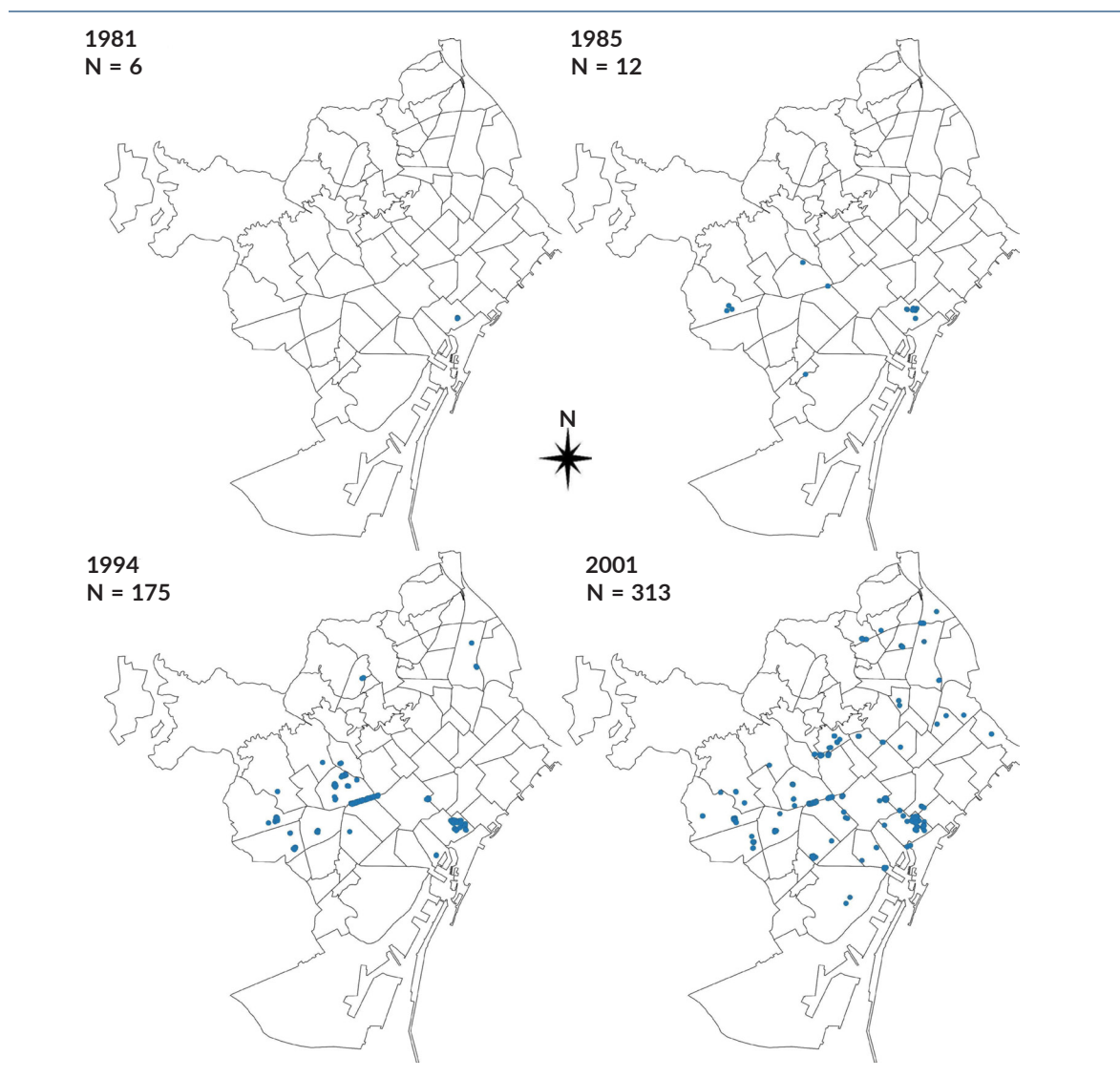
be used for sleeping by a variable number of individuals each day, and as not all chambers are in use within a given breeding season (Navarro et al 1992, Eberhard 1998), we used the average number of individuals per chamber, as previously estimated in other studies (Domènech et al 2003, Pascual et al 2015). To calculate these figures the authors monitored the arrivals and departures of individuals in each chamber from two hours before sunset (i.e., before the parakeets began to return to their nests) until the end of bird activity. The population size was obtained by multiplying the total number of chambers by the average number of individuals sleeping per chamber. These mean values were 1.62 (SD = 1.3) for the years 1976 to 1994 (Senar and Domènech, pers. comm.); 1.52 (SD = 1.8) for 1999 to 2001 (Domènech et al 2003) and 1.47 (SD = 1.17) for 2010 to 2022 (Pascual et al 2015). These conversion factors did not exhibit significant differences between years; thus, we used their average across all years (average factor = 1.53). Additionally, we tested whether the number of chambers per nest changed over time with an ANOVA.

The population growth rate was estimated by fitting four functions: linear, exponential, logistic, and Weibull. The first two functions assume continuous growth, while the logistic and Weibull functions account for potential stabilisation in observed population growth (Gotelli 2001, Duncan et al 2014). Model fits were compared using Akaike's Information Criterion (AIC), where the lowest AIC value was considered the best. Additionally, Pearson's correlation value between real and estimated data, according to each function, was used as an additional measure of fit. Since the analyses revealed that population growth for most of the studied period fit an exponential function, we investigated further assuming exponential growth. To do so, we used the natural logarithm of the population size, which had been previously calculated for each year. The slope of the regression between year and $\ln(\text{population size})$ represents the population growth rate (r) (Gotelli 2001). The time it takes for a population to double in size (population doubling time) was estimated by $\ln(2)/r$ (Brauer and Castillo-Chávez 2012).

To calculate the expansion area in each year, we drew a 500x500 m grid on the map using the 'create grid' vector tool in QGIS and counted the number of squares occupied by nests. Then, the number of occupied squares was multiplied by the area of each square to obtain the occupied area. Finally, using the square root of the occupied area and the years since colonisation, a linear regression was fitted. A good fitting means that the population is dispersing at a constant rate (diffusion model) (Gotelli 2001). We performed all data pre-processing and obtained summary statistics using R version 3.6.3 (R Core Team, 2020) and used the ggplot2 package version 3.3.2 (Wickham 2016) to create figures.

Results

We have reconstructed the invasion history of monk parakeets in Barcelona city both in population size



and range expansion from 1976 to 2022. During this period, monk parakeets spread all over the Barcelona area (fig. 1).

The first nest of monk parakeets in Barcelona was detected in 1976 in Poblenou cemetery, close to Ciutadella Park, but was removed by the municipal services (see introduction). The second nest was detected in 1979 in Ciutadella Park, in the garden adjacent to the Aviariu of the Zoological Garden (Zoo) (S. Filella pers. comm.). The first survey on the species, performed in 1981, detected the first colony of the species, with six nests established in Ciutadella Park, in the same garden in the Zoo that attracted the second nest recorded (fig. 1, 1981). Since 1981, the species not only spread all over the city but the population size grew continuously (fig. 2). This increase can be seen both in the number of individuals and in the number of nests and chambers (table 1). The number of chambers per nest changed over time ($F_{14} = 8.63, p < 0.001$), although the variation was not extreme.

The fit of the observed population growth to the various population growth models and their comparisons are shown in table 2 for all years (1976 to 2022), where the best fit was for the Weibull population growth function. However, when the models were fitted excluding the data from 2022, the best adjustment was for the exponential population growth function (table 3).

Assuming therefore an exponential growth for the whole period (fig. 3), we calculated a population growth rate for the period 1976-2022 of $r = 0.19$ (fit to the exponential curve, $R^2 = 0.85, p < 0.0001$), which means a population doubling time of approximately four years (3.7 years). The size of the population estimated for the year 2022 in Barcelona was $6,444 \pm 449$ individuals.

However, a closer inspection of figure 3 suggested that we can distinguish two phases in the population growth of monk parakeets in Barcelona city. From the beginning and until 1994 the population growth rate

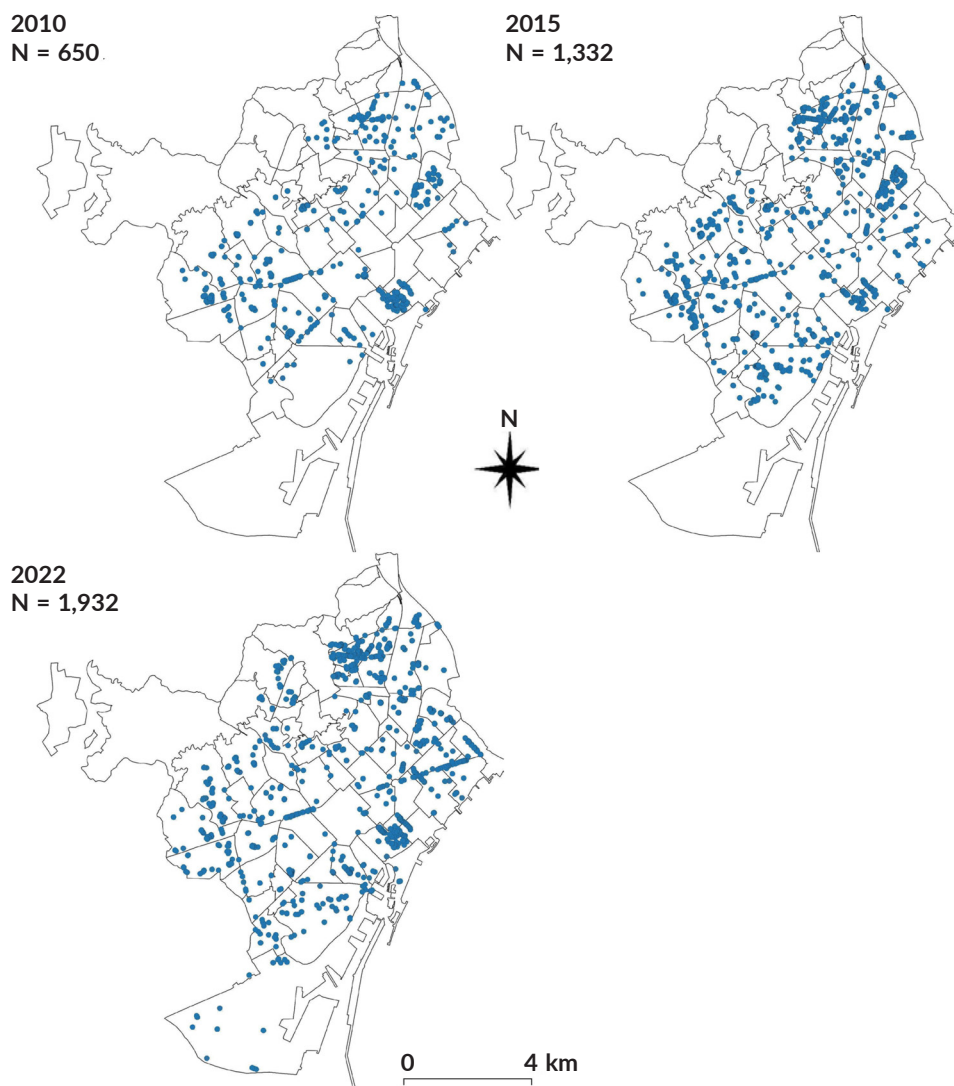


Fig. 1. Expansion map of the monk parakeet in Barcelona city. Blue points represent the exact location of the nests for each year: N, total number of nests. (The divisions within the city are the neighbourhoods).

Fig. 1. Mapa de la expansión de la cotorra argentina en la ciudad de Barcelona. Los puntos azules indican la ubicación exacta de los nidos cada año: N, número total de nidos. (Las líneas divisorias delimitan los barrios de la ciudad).

was constant and with a steep slope with an exponential growth rate of $r = 0.37$ ($R^2 = 0.97$, $p < 0.0001$, fig. 4 left) and a population doubling time of approximately two years (1.9 years). Then, from 1999 to 2022, the exponential growth was less pronounced, but still exponential, with a growth rate of $r = 0.08$ ($R^2 = 0.97$, $p < 0.01$, fig. 4 right) and a population doubling time of nine years (9.0 years).

The analysis of the spread across the city showed a close fit to a line for the regression of the square root of the total area occupied to years since colonisation, which strongly suggests that occupation of space over time followed a diffusion model ($R^2 = 0.98$, $p < 0.0001$, fig. 5).

Discussion

In this study, we used historical data of the presence of monk parakeets in Barcelona city to assess the population growth rate and range expansion of the species. Overall, we found that (i) the population of monk parakeets showed a sustained exponential increase over the study period (1976-2022), reaching a population size of $> 6,400$ birds by 2022, (ii) the population exhibited two growth periods, both characterised by exponential high growth rates, and (iii) there was a sustained range expansion following a diffusion model.

The differences in the number of chambers over the years may be due to the fact that at the begin-

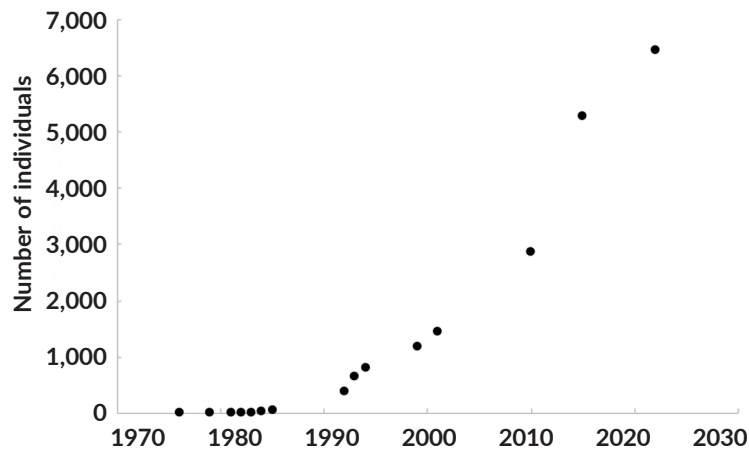


Fig. 2. Evolution of the number of monk parakeet individuals in the city of Barcelona 1976-2022.

Fig. 2. Evolución del número de ejemplares de cotorra argentina en la ciudad de Barcelona entre 1976 y 2022.

ning of the expansion, there were few parakeets, so their nests mostly contained only one chamber. As the population increased, the number of nests and chambers also grew since the offspring of the first and second generations tended to stay close to their relatives, building new chambers onto the existing nests (Dawson-Pell et al 2021). This increase in the number of chambers per nest in the 1990s was also accompanied by little or no control by municipal services over the nests (pers. obs.), with a single nest reaching up to 36 chambers in 2001. From that year onwards, the city council began to intervene in

nests due to the risk of them falling, especially the largest ones, which caused the average number of chambers to decrease. However, some nests with a low risk of collapse, either due to their location or type of substrate, continued to grow. This explains why the maximum number of chambers can still be high in recent years, even though the nests are controlled and the average number of chambers has decreased.

Estimates of population size suggest that there has been exponential growth since the detection of the first nest. This contrasts with data from

Table 1. Number of nests and chambers (with mean, SE, median, minimum and maximum) per year of monk parakeets in Barcelona city.

Tabla 1. Número de nidos y cámaras (con la media, el EE, la mediana, el mínimo y el máximo) por año de cotorra argentina en la ciudad de Barcelona.

Year	Nests	Chambers	Mean	SE	Median	Min	Max
1976	1	1	1.00		1.0	1	1
1979	1	1	1.00		1.0	1	1
1981	6	6	1.00	0.00	1.0	1	1
1982	7	7	1.00	0.00	1.0	1	1
1983	11	12	1.09	0.09	1.0	1	2
1984	12	23	1.91	0.42	1.5	1	6
1985	19	35	1.84	0.29	1.0	1	6
1992	77	255	3.31	0.29	3.0	1	16
1993	125	429	3.58	0.19	3.0	1	10
1994	175	523	3.06	0.16	2.0	1	13
1999	271	779	2.87	0.13	2.0	1	16
2001	313	948	3.07	0.21	2.0	1	36
2010	650	1,876	2.66	0.11	2.0	1	20
2015	1,332	3,449	2.59	0.07	2.0	1	22
2022	1,932	4,212	2.18	0.04	2.0	1	20

Table 2. Comparison of AIC and Pearson correlation for fitting different growth functions to the monk parakeet population in the city of Barcelona from 1976 to 2022 (t is the statistical value of the t-test and df are the degrees of freedom).

Tabla 2. Comparación del criterio de información de Akaike y la correlación de Pearson para ajustar diferentes funciones de crecimiento a la población de cotorra argentina en la ciudad de Barcelona entre 1976 y 2022 (t es el valor estadístico de la prueba t y df son los grados de libertad).

Model	Pearson correlation (df = 12)				
	AIC	ΔAIC	Correlation	t	p-value
Weibull	4.70	0.00	0.995	34.72	< 0.001
Exponential	21.25	16.55	0.981	17.58	< 0.001
Linear	34.72	30.02	0.941	9.67	< 0.001
Logistic	67.02	62.32	0.941	9.66	< 0.001

Table 3. Comparison of AIC and Pearson correlation for fitting different growth functions to the growth of the monk parakeet population in the city of Barcelona from 1976 to 2015 (hence excluding 2022) (t is the statistical value of the t-test and df is the degrees of freedom).

Tabla 3. Comparación del criterio de información de Akaike y la correlación de Pearson para ajustar diferentes funciones de crecimiento al crecimiento de la población de cotorra argentina en la ciudad de Barcelona entre 1976 y 2015 (el año 2022 queda excluido) (t es el valor estadístico de la prueba t y df son los grados de libertad).

Model	Pearson correlation (df = 11)				
	AIC	ΔAIC	Correlation	t	p-value
Exponential	-3.35	0.00	0.994	30.10	< 0.001
Weibull	1.66	5.00	0.993	28.34	< 0.001
Linear	28.92	32.27	0.918	7.69	< 0.001
Logistic	54.91	58.26	0.941	7.69	< 0.001

other exotic birds such as lavender waxbill *Estrilda caeruleus*, red avadavat *Amandava amandava*, red-vented bulbul *Pycnonotus cafer*, red-whiskered bulbul *Pycnonotus jocosus* or rose-ringed parakeet *Psittacula krameri* (Aagaard and Lockwood 2014). In those species and in contrast with our monk parakeet population in Barcelona, a lag phase was detected. This lag-phase typically lasts several years, until the species adapts to the new conditions of the place of introduction (Hui and Richardson 2017, Kelly et al 2021). Although this lag-phase is not seen in our data, it should be considered that between the first observation of individuals in the early 60s, as a result of escapes from cages or releases by different people (Ferrer 2016), and

the first nest detected in 1976, this lag phase could most probably have occurred in which some individuals were in the area for several years while they adapted to the city of Barcelona before building the first nest. Additionally, it is possible that during the incipient invasion the detectability of the nests would have been less efficient given the lack of knowledge of this invasive species. Furthermore, it is also possible that there were already nests in Barcelona, although not in public spaces, but, for example, in private residences, which would make detectability less effective, and thus underestimate the early stages of the invasion.

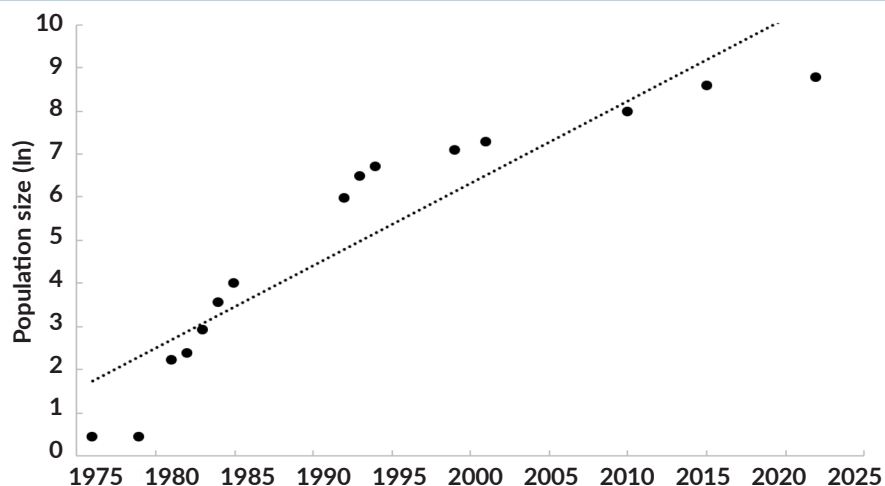


Fig. 3. Exponential growth of the monk parakeet population in Barcelona city from 1976 until 2022.

Fig. 3. Crecimiento exponencial de la población de cotorra argentina en la ciudad de Barcelona entre 1976 y 2022..

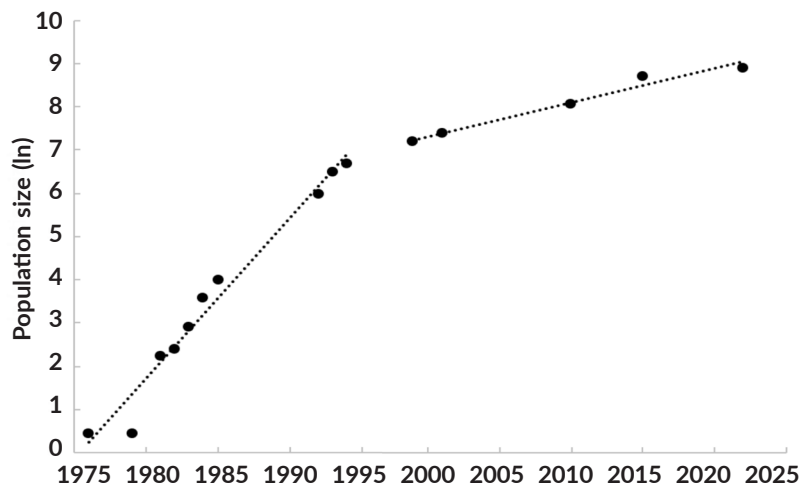


Fig. 4. Exponential growth of the monk parakeet population at two different speeds in Barcelona city. Left, from 1976 to 1994, and right from 1999 to 2022.

Fig. 4. Crecimiento exponencial de la población de cotorra argentina en dos velocidades diferentes en la ciudad de Barcelona. A la izquierda, entre 1976 y 1994 y a la derecha, entre 1999 y 2022.

With respect to the Weibull model adjustment, we found for population growth over time using all available data, we believe that data from future years is necessary to determine whether the population is truly beginning to stabilise or if the lower population size estimated in 2022 is merely a random effect. Another reason for a decrease in population growth in more recent years could be a matter of spatial scale since we have measured population growth within the city of Barcelona, but we know that the population has already spread beyond the limits of the city, occupying other municipalities adjacent to

Barcelona, such as Hospitalet, Santa Coloma and Badalona. Here new questions are opened for future studies in order to ascertain whether population growth is truly decreasing in Barcelona but increasing outside the city limits, or if the population expansion occurs mainly near the leading edge of the expansion or not.

The overall growth rate in Barcelona and the population doubling time is similar to that of the total population of these parakeets in Spain from 1997 to 2002, with a growth rate of 0.18 and a population doubling time of 3.9 years (Muñoz 2003). We can find examples of population growth values similar

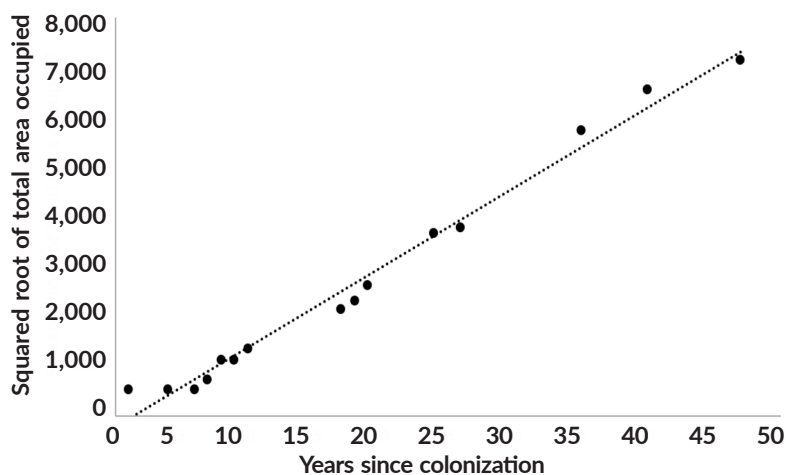


Fig. 5. Expansion range of the monk parakeet over the years since its colonization in Barcelona city. (Year 1: 1976).

Fig. 5. Área de distribución de la cotorra argentina a lo largo de los años desde que colonizó la ciudad de Barcelona. (Año 1: 1976).

to other sites on the Iberian Peninsula. In Madrid the population growth rate from 2005 to 2015 was estimated at 0.31, with a population doubling time of 2.3 years (Molina et al 2016). These values for Madrid are similar to those of the first period in Barcelona (fig. 4, left), where the growth rate was 0.37 and the population doubling time was around two years. Additionally, the population growth rate in Malaga (Spain) from 1995 to 2019 was estimated at 0.19, with a population doubling time of 3.7 years (López-Ramírez and Muñoz 2022), similar to the total values obtained for Barcelona.

Compared to other countries, the growth rates in Italy (0.19) and UK (0.17) are similar to those of Barcelona. However, the values are considerably larger in Greece, where the population growth rate is 0.42, and the population doubling time is 1.7 years (Postigo et al 2019), being similar to the data from the first period in Barcelona (fig. 4, left). In contrast, the growth rate in France of 0.08 and the population doubling time of 7.7 years are similar to those of the second growth period in Barcelona (fig. 4, right), where the growth rate is 0.08 and the population doubling time is nine years. In North America, the values follow a trend similar to the general trend for Barcelona. The average annual rate of population growth for the United States from 1971 to 1995 was 0.15, with a population doubling time of 4.8 years (van Bael and Pruett-Jones 1996), similar to the population in Barcelona.

Regarding the growth rates of other invasive species, the value of the monk parakeet population in Barcelona is similar to that of the red-whiskered bulbul *Pycnonotus jocosus* population in Valencia, which has a growth rate of 0.15 (Domínguez-Pérez and Gil-Delgado 2022), and that of the rose-ringed parakeet in Tenerife, which has a population growth rate of 0.21 between 2014 and 2019 (Hernández-Brito et al 2022a). In Seville, the growth rate of rose-ringed parakeets is much higher than that of monk parakeets in Barcelona, with a value of 0.81 and therefore a population doubling time of almost one year (Hernández-Brito et al 2022b). This growth of the rose-ringed parakeet population in Seville adjusts to a quadratic temporal trend (logistic growth) rather than an exponential.

Our population shows two different periods of exponential growth, shown in figure 4; in both periods the natural logarithm of the population size again increases linearly with time. This pattern with two phases has been evidenced in other species, such as the muskrat *Ondatra zibethicus*, which displayed two periods in its range expansion (van den Bosch et al 1992). However, unlike the case of the muskrat, this difference in the speed of the monk parakeet population wave in two periods is not caused by an effective trapping program since the monk parakeet population in Barcelona city is not yet controlled. We do not know what alternative mechanism caused the population growth rate to slow down since 2000. One potential explanation is negative density dependence, although we have no direct evidence for reduced survival or productivity of monk parakeets since that time.

The range expansion of monk parakeets in Barcelona (fig. 1, 5) is consistent with other invasions of exotic

bird species that can approach exponential population growth and show a corresponding expansion of their range (Blackburn et al 2009), the former being the precursors of the latter (Veit and Lewis 1996). The increase in range fits a diffusion model, providing a good basis to describe this pattern (Hastings et al 2005, Bonneau et al 2016, Hui and Richardson 2017), in which the spread of populations through empty sites is analogous to the dispersion of an ink droplet through a beaker of water (Gotelli 2001). It is known that in the first phases of growth of the monk parakeet population in Barcelona there was a contagious distribution, but that as of 2015 they have expanded much more to new places (Núñez-Tobajas et al 2023). Taking into account its presence in the nearby extralimital areas, we can assume that its distribution will continue to spread in the area if measures are not taken now. It can already be seen how some monk parakeet individuals have dispersed long-distance outside of Barcelona, to distances of 10 to 70 km (Borray-Escalante et al 2023).

The increase in population size of the monk parakeet shows that individuals easily find resources that allow them to survive, reproduce and invade new areas. There are several factors that could have led to the success of their invasion in Barcelona, including the breadth of their diet, the abundance of food and the availability of abundant old trees such as palm trees *Phoenix* species, plane trees *Platanus* species, pines *Pinus* species, cedars *Cedrus trees* or cypresses *Cupressus* trees, which are the main substrates for parakeets nests in the city (Núñez-Tobajas et al 2023). In effect, it is known that parakeets in Barcelona are more abundant in neighbourhoods with a high density of trees and a high percentage of people over 65 years of age (Rodríguez-Pastor et al 2012). This has been attributed to the parakeets needing trees as a food source and nesting site, and to older people often feeding the species (Rodríguez-Pastor et al 2012, Borray-Escalante et al 2020). In addition, part of the success of the species is due to its great reproductive potential: the reproductive success of the species in Spain is double that of its areas of origin, the percentage of pairs that attempt a second clutch is triple and 55% of birds reproduce in their first year, while in South America almost no one year-olds reproduce (Senar et al 2019). Other reasons could be the monk parakeet's resistance to parasites or viruses (Mori et al 2019, Martínez-de la Puente et al 2020, Blanco-González et al 2023). This parakeet is also unique among parrots in that they build their own nests from twigs instead of relying on holes like other species of parrots. Furthermore, they often breed in colonies, with many nests often occupying the same tree (Dawson-Pell et al 2024). Consequently, nesting sites are not a limiting factor. As a result, the growth rate of the invasive monk parakeet population does not appear to be currently limited by predators, resources, disease, or nest-site availability, and is expected to continue to increase and expand its range if control measures are not taken in the near future. Therefore, it is essential to develop a surveillance and control program that includes measures that are evaluated periodically in

order to be efficient, thus reducing the impacts of the species. For this, it will be important that in order to improve global well-being the program is designed to address the impact on animal health, human health, and the health of the environment.

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Author contributions

NA Borray-Escalante, BJ Hatchwell, L Cardador, T Montalvo, JC Senar designed the study. X Batllori, D Santos, J Clavell, J Domènech, L Arroyo, F Uribe, R Rodríguez-Pastor, J Pascual, JG Carrillo-Ortiz, B Molina, JC del Moral, Z Nuñez-Tobajas, T Montalvo, NA Borray-Escalante, JC Senar conducted the censuses. NA Borray-Escalante, BJ Hatchwell, L Cardador, JC Senar analysed the data. NA Borray-Escalante, BJ Hatchwell, JC Senar wrote the paper with input from all authors. All authors read and approved the final manuscript.

Conflicts of interest

No conflicts declared.

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Complete affiliations

NA Borray-Escalante, Z Nuñez-Tobajas, X Batllori, J Domènech, L Arroyo, F Uribe, R Rodríguez-Pastor, J Pascual, JG Carrillo-Ortiz, JC Senar, Museu de Ciències Naturals de Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain.

NA Borray-Escalante, L Cardador, Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.

R Rodríguez-Pastor, Department of Parasitology, Veterinary Faculty, University of Zaragoza, c/ Miguel Servet 177, 50013 Zaragoza, Spain; and Instituto Agroalimentario de Aragón-IA2, University of Zaragoza, c/Miguel Servet, 177, 50013 Zaragoza, Spain.

D Santos, J Clavell, Grupo de Aves Exóticas, SEO/BirdLife, c/Melquíades Biencinto 34, 28053 Madrid, Spain.

T Montalvo, Agència de Salut Pública de Barcelona, Pl. Lessep 1, 08023 Barcelona, Spain; and CIBER Epidemiología y Salud Pública (CIBERESP), c/Monforte de Lemos 5, 28029 Madrid, Spain.

B Molina, JC del Moral, Estudio y seguimiento de aves SEO/BirdLife, c/Melquíades Biencinto 34, 28053 Madrid, Spain.

B Hatchwell, Dept. of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.