Journal of Caribbean Ornithology

RESEARCH ARTICLE Vol. 36:114–125.2023

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Photo: Ken Pinnow

BirdsCaribbean

Journal of Caribbean Ornithology
Research Article Vol. 36:114–125. 2023
jco.birdscaribbean.org ISSN 1544-4953 https://doi.org/10.55431/jco.2023.36.114-125
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# Population increase and range expansion of White-winged Parakeets (*Brotogeris versicolurus*) in Puerto Rico

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Associate Editor: Clint Boal

Cover Page: White-winged Parakeet (*Brotogeris versicolurus*) on anacagüita tree (*Sterculia apetala*) in Rincón, Puerto Rico on 2 February 2021. Photographer: Ken Pinnow.

Published: 3 October 2023

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## Abstract

Puerto Rico has experienced multiple introductions of Psittaciformes that have established self-sustaining populations, and the White-winged Parakeet (*Brotogeris versicolurus*) has been considered the most successful introduced psittacine species on the island. In this study, we evaluated their population size, calculated growth rates, and estimated the breeding proportion in two populations by performing roost counts for four consecutive years in addition to evaluating their range expansion. We also assessed their diet and breeding ecology. Population estimates of the parakeets during the study period showed a steady increase, with a maximum of ca. 3,010 individuals (± 673 SD) in the San Germán population, and ca. 3,128 individuals (± 762 SD) in the San Patricio population. Both populations exhibited a geometric mean population growth rate of 1.25 per year. As expected, the data indicates that the populations experienced a lag-phase prior to exponential growth. This is supported by the island-wide sighting trends and range expansion. Moreover, we detected range expansion during our study through the colonization of new areas. The population estimates and population growth rates, along with the sighting trends and their wide distribution, makes the White-winged Parakeet the most successful psittacine species in Puerto Rico. The factors leading to their invasion success are likely to include propagule pressure, their diet breadth, and their capability as primary nesters in the abundant termite mounds on the island. Currently, the growth rate of the invasive White-winged Parakeet population does not appear to be limited by predators, resources, or nest availability, and we expect them to continue increasing and expanding their range.

## Keywords

biological invasions, *Brotogeris versicolurus*, islands, population growth, Psittacidae, Puerto Rico

## Resumen

**Incremento poblacional y expansión de la distribución del perico aliblanco (*Brotogeris versicolurus*) en Puerto Rico** • Puerto Rico ha experimentado múltiples introducciones de Psittaciformes, los cuales han establecido poblaciones autosostenibles, y *Brotogeris versicolurus* ha sido considerada la especie de psitácida introducido más exitosa en la isla. En este estudio, evaluamos sus tamaños poblacionales, calculamos sus tasas de crecimiento y estimamos la proporción de individuos reproductores mediante la realización de conteos de dormideros por cuatro años consecutivos en dos poblaciones. Además, evaluamos la expansión de su área de distribución y su dieta y ecología reproductiva. Las estimaciones de la población de pericos durante el periodo de estudio mostraron un aumento constante, con un máximo de unos 3.010 individuos (± 673 DE) en la población de San Germán, y de unos 3.128 individuos (± 762 DE) en la población de San Patricio. Ambas poblaciones mostraron una tasa media geométrica de crecimiento poblacional de 1.25 individuos por año. Como era de esperar, los datos indican que las poblaciones experimentaron una fase de latencia ("lag-phase") antes del crecimiento exponencial. Las tendencias de avistamiento en toda la isla y la expansión del área de distribución respaldan esta afirmación. Además, durante nuestro estudio detectamos una expansión del área de distribución mediante la colonización de nuevas zonas. Las estimaciones poblacionales y las tasas de crecimiento de la población, junto con las tendencias de avistamiento y su amplia distribución, convierten a *Brotogeris versicolurus* en la

## Cite this article as:

Falcón, W., and R.L. Tremblay. 2023. Population increase and range expansion of White-winged Parakeets (*Brotogeris versicolurus*) in Puerto Rico. Journal of Caribbean Ornithology 36:114–125. https://doi.org/10.55431/jco.2023.36.114-125

especie de psitácida de mayor éxito en Puerto Rico. Los factores que han contribuido a la invasión de Pericos aliblancos posiblemente incluyen la presión de propágulo, su amplitud de dieta, y su capacidad como anidadores primarios en montículos arbóreos de termitas, los cuales son abundantes en la isla. Actualmente, la tasa de crecimiento de la población invasora de esta especie no parece estar limitada por depredadores, recursos o disponibilidad de nidos, y esperamos que siga expandiendo su área de distribución.

## Palabras clave

*Brotogeris versicolurus*, crecimiento poblacional, invasiones biológicas, islas, Psittacidae, Puerto Rico

## Résumé

**Augmentation de la population et expansion de l'aire de répartition du Toui à ailes variées (*Brotogeris versicolurus*) à Porto Rico •** Porto Rico a connu de nombreuses introductions d'espèces de Psittaciformes, qui ont établi des populations autonomes, et le Toui à ailes variées (*Brotogeris versicolurus*) est considéré comme le psittacidé introduite le plus prospère sur l'île. Dans la présente étude, nous avons estimé la taille des populations de Toui à ailes variées, calculé les taux de croissance et évalué la proportion de la population qui se reproduise dans deux populations, en effectuant des comptages au dortoir pendant quatre années consécutives, ainsi qu'une évaluation de l'expansion de leur aire de répartition. Nous avons également évalué le régime alimentaire et l'écologie de reproduction de l'espèce. Les estimations des populations au cours de la période d'étude ont mis en évidence une augmentation constante, avec un maximum d'environ 3 010 individus (écart-type ± 673) dans la population de San Germán, et d'environ 3 128 individus (écart-type ± 762) dans la population de San Patricio. Les deux populations ont connu une croissance moyenne géométrique de 1,25 par an. Comme prévu, les données indiquent que les populations ont traversé une phase de latence avant de croître de manière exponentielle. Cela est confirmé par les tendances des observations sur l'ensemble de l'île et par l'expansion de l'aire de répartition. Au cours de notre étude, nous avons détecté une expansion de l'aire de répartition en observant la colonisation de nouvelles regions. Les estimations et les taux de croissance des populations, ainsi que les tendances des observations et la large répartition de l'espèce, font du Toui à ailes variées le psittacidé le plus prospère à Porto Rico. Les facteurs qui ont contribué à cette invasion sont probablement la pression exercée par les individus colonisateurs, la diversité de leur régime alimentaire et leur capacité à nicher dans les nids de termites arboricoles qui sont nombreux sur l'île. Actuellement, le taux de croissance des populations envahissantes de Toui à ailes variées ne semble pas être limité par les prédateurs, les ressources alimentaires ou la disponibilité des nids, et nous prévoyons que cette espèce continue d'augmenter et d'étendre son aire de répartition.

## Mots clés

*Brotogeris versicolurus*, croissance de la population, îles, invasions biologiques, Porto Rico, Psittacidae

Non-native invasive species are viewed as a significant component of global biological change (Vitousek *et al.* 1996), and often have negative impacts on native species, communities, and ecosystems (Luque *et al.* 2014). Different 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). Whether they become invasive (sensu Blackburn *et al.* 2011) or not depends on a myriad of factors, e.g., propagule pressure (Von Holle and Simberloff 2005), pre-adaptive characters (Sol 2008), and facilitation by other species (Helms and Vinson 2003). Two main processes characterize invasive species: exponential population growth and range expansion, and these are often preceded by a lag-phase (period during which organisms adapt to the new habitat and where there is little population increase; Sakai *et al.* 2001). Understanding the link between population growth and range expansion may help in developing management strategies for invasive species.

Birds are among the most widely introduced taxonomic groups across the world (Blackburn *et al.* 2009). Several modes of introductions to non-native habitats have been responsible for avian establishment, e.g., accidental releases (Blackburn *et al.* 2009) and releases by acclimatization societies (Eguchi and Amano 2004, Duncan *et al.* 2006). Additionally, in recent times, the pet trade is one of the most common modes of introduction of invasive bird species (e.g., Carrete and Tella 2008, Russello *et al.* 2008, Cassey *et al.* 2015, Falcón and Tremblay 2018). Exotic bird species regarded as invasive may often approximate exponential population growth and show range expansion (Blackburn *et al.* 2009), with the former serving as a precursor to the latter (Veit 1997). Among birds, Psittaciformes in particular have been favorably and highly traded in the pet market and, as a result, psittacine species are one of the most successful groups of birds to establish populations outside their native range (Cassey *et al.* 2004).

Perhaps the most widely known invasive species of psittacines are the Monk Parakeet (*Myiopsitta monachus*) and the Rose-ringed Parakeet (*Psittacula krameri*). As with invasive birds in general, invasive populations of Monk Parakeets in the USA and Spain have exhibited exponential growth, with an estimated annual population increase of 15% between 1972–1995 (Van Bael and Pruett-Jones 1996) and 8% between 1994–2001 (Domènech *et al.* 2003) respectively. In the USA, even after a control program attempt, both the abundance and range of Monk Parakeets were increasing exponentially (Blackburn *et al.* 2009). Similarly, Rose-ringed Parakeets exhibiting exponential population growth and aggressive range expansion have been recorded (Nebot 1999, Butler 2003, Kleunen *et al.* 2010, Dodaro and Battisti 2014).

Puerto Rico has experienced perhaps the highest rate of introduction of parrots in the wild (Falcón and Tremblay 2018), and the White-winged Parakeet (*Brotogeris versicolurus*) has been considered the most successful psittacine species established on the island (Pérez-Rivera *et al.* 1984, Raffaele 1989, Camacho-Rodríguez *et al.* 1999, Oberle 2000). Although Pérez-Rivera *et al.* (1984) warned that the White-winged Parakeet could expand and cause significant damage to crops, there is no evidence of crop damage yet (Falcón and Tremblay 2018). Previous surveys have confirmed the persistence of locally common and self-sustaining populations of the White-winged Parakeet (Pérez-Rivera *et al.* 1984, Raffaele 1989, Camacho-Rodríguez *et al.* 1999, Oberle 2000). Since 2004, 35 years after the species was first reported in the wild in Puerto Rico, populations of White-winged Parakeets occupy a wide range on the island (Falcón and Tremblay 2018). This brought renewed concerns about the possible negative effects that the parakeet might have on the native flora and fauna, and on the agricultural sector, if the species kept expanding its range.

The White-winged Parakeet is considered a widespread species in its native range of South America, occupying French Guiana, the Amazon basin from the north of Brazil to the south-east of Colombia, east of Ecuador, north of Argentina and Paraguay, and the south-east of Brazil (Forshaw 1973). Its non-native range includes Ecuador (west of Los Andes; Freile *et al.* 2012), California (Arrowood 1981), and Florida (Juniper and Parr 1998, Forshaw 2010). Moreover, in 1969, Kepler made the first report of feral White-winged Parakeets in Puerto Rico, in the area of Luquillo (Bond 1971), and since then, others have reported its presence and persistence on the island (Pérez-Rivera *et al.* 1984, Raffaele 1989, Camacho-Rodríguez *et al.* 1999).

White-winged Parakeets are mainly frugivorous, although they may also use nectar and seeds as part of their diet (Janzen 1981, Pérez-Rivera *et al.* 1984, Francisco *et al.* 2002). Many psittacines, including this species, roost communally (Juniper and Parr 1998, Brightsmith *et al.* 2017). The White-winged Parakeet nests in arboreal termite mounds and sometimes in tree cavities (Pérez-Rivera *et al.* 1984). Moreover, we observed that in Puerto Rico, a proportion of the roosting population presumably break up into pairs and breed from late December to May and then eventually re-join the non-breeding roosting proportion of the population. This was confirmed by Tossas *et al.* (2012) in a population in San Germán, Puerto Rico and has also been reported in the native range (Forshaw 1973, Juniper and Parr 1998). In the continental U.S., fledglings have been reported to stay with the parents and return to the roosting sites after the breeding season (Schroads 1974, Arrowood 1981). In California, the parakeets have shown roosting site fidelity (Arrowood 1981), and in Florida, seasonal and annual shifts in roost sites have been reported (Schroads 1974). The birds were not marked in any of the previous studies, so it is unknown if this involves the same individuals across time (Brightsmith *et al.* 2017).

In this study, we assess the invasive ecology of the White-winged Parakeet, including population estimates, population growth rates, range expansion, and natural history. In concordance with the wide range of habitats occupied by this species on the island (described by Falcón and Tremblay 2018), we expected to find evidence of exponential population growth rates and range expansion. We also address the possible factors that may have contributed to the establishment success of White-winged Parakeets in Puerto Rico.

## Methods

### Population ecology of the White-winged Parakeet

To estimate the roosting population size, we used the "Point Counts for Parrots" method as described in Wunderle (1994), which is appropriate for Psittaciformes (Chapman *et al.* 1989, Gnam and Burchsted 1991, Pithon and Dytham 1999, Tossas *et al.* 2012). In general, birds are counted simultaneously at the roost by several observers that count the passing birds and record the time and compass bearing of their flight. This information is then compared between observers and used to eliminate duplication (double counting; observers at different locations are likely to count some of the same birds).

In Puerto Rico, during the study period (2006–2010), White-winged Parakeets were especially abundant in the Metropolitan Area of San Juan (north-east) and in the south-west of the island. During the non-breeding season of 2006, we followed flocks before dusk to identify the roosting sites in each area. We identified one roosting site in each area where a sizeable quantity of parakeets would roost. The choice of monitoring the selected sites were based on accessibility and clear view of the roosting sites for maximizing the point counts. The roost of the north-east population was located within the San Patricio shopping mall area in the municipality of Guaynabo (18°24'24.9"N, 66°06'11.7"W), and had never been reported in the literature before (although flocks have been reported in the area as early as 1981; Pérez-Rivera *et al.* 1984). The roosting area of San Patricio consisted of planted aggregated Royal palms (*Roystonea* sp.) and a single Mahogany tree (*Swietenia mahogani*) within the shopping mall area. The south-west population roost was located within the Interamerican University Campus in the municipality of San Germán (18°04'57.7"N, 67°02'55.6"W). It was first reported present by 1968 (Pérez-Rivera *et al.* 1984) and has persisted throughout the years (Pérez-Rivera 1992 cited in Tossas *et al.* 2012, Raffaele and Kepler 1992 cited in Tossas *et al.* 2012, Camacho-Rodríguez *et al.* 1999, Tossas *et al.* 2012). The roosting site of San Germán consisted of three planted aggregated Antilles calophyllum (*Calophyllum antillanum*) next to a parking lot within the campus.

The fragmented vegetation of both sites, as well as the terrain and building features, allowed us to identify areas from which the birds could be readily observed entering or leaving the roosting area. Counts were conducted by two observers, each covering 180° of the roosting sites at delimited points surrounding the roosting area. The monitoring period started at dawn in San Patricio (with birds leaving the roost) and before dusk in San Germán (with birds entering the roost) and stopped after 20 minutes with no birds departing or entering the roost area. Because the birds gather in flocks and fly in different directions from or to the roosting area, each observer counted birds flying out of or into the roosting area in different directions to avoid double counting. In other words, if any bird returned to (San Patricio) or left (San Germán) the roosting area, it was subtracted from the count values, as they would ultimately return to (San Patricio) or depart from (San Germán) the area again (and be counted), thus avoiding double counting. We used SLR cameras with telephoto lenses (70–300 mm) to photograph the flocks and then counted the quantity of individuals for large flocks (> 16 individuals) from the photos. Days with inclement weather that resulted in difficulty in counting the birds were avoided and counts were repeated if necessary. Non-breeding roost counts (representing the minimum population size) in the San Patricio population were conducted in September of each year (2007–2009, but in 2010 it was conducted in November due to rains), and the counts in the San Germán population were conducted in October of each year (2007–2010). In 2010, we performed breeding roost counts during late March (mid-late breeding season) in both roosting populations to estimate the proportion of breeding birds. To determine the proportion of the breeding population, we subtracted the number of parakeets counted during the breeding censuses of 2010 from the population estimates of the 2009 non-breeding censuses. Since both adults have been reported to roost in the nest until all chicks are fledged (Schroads 1974), we divided the total number of breeding individuals by two to get the approximate number of breeding pairs. To test the effectiveness of our count method and its error rate, we conducted three roost counts spaced a week apart from September to October 2007 in the San Patricio population.

For the estimates of population size and growth rates, we assumed that 1) all the parakeets roosted communally during the non-breeding season and that during the breeding season, only non-reproductive parakeets roosted communally; 2) the parakeets returned to roost in the same area after the breeding season; 3) the counts that were performed during the non-breeding season reflected the population size after mortality and emigration events shortly after the breeding season; 4) the number of parakeets counted in each roost is accurate; and 5) the estimated population size represents the minimum number of parakeets in the roost.

We calculated the population growth rates using the equation for exponential growth in populations with overlapping generations (Equation 1; Rockwood 2015) re-arranged as

$r = \ln(N_t / N_0)/t$ to get the $r$ values, where:
$r$ is the intrinsic rate of increase;
$N_t$ is the population size at time $t$;
$N_0$ is the initial population size;
$t$ is the time in years.

This model assumes that 1) the population has overlapping generations and that 2) the population exhibits a stable age structure. In this model, the population grows if $r > 0$, decreases if $r < 0$, and is static if $r = 0$. We then converted the $r$ values to the finite rate of increase per year, with the equation $\lambda = e^r$. When $\lambda < 1$, the population decreases, the population is stable if $\lambda = 1$, and the population increases if $\lambda > 1$.

To compare the roosting counts with sighting trends across the island, we used count observation reports from eBird (eBird 2021) analyzed in Falcón and Tremblay (2018). eBird is an open access observational database that supports evidence-based research, conservation, and management actions in a cost-effective way, particularly in the absence of scientifically-derived data (Sullivan *et al.* 2017). Data provided in eBird include the date and time of the observation, the location of the observation, and the number of individuals observed. We assessed the island-wide sighting trends by calculating the sum of the mean number of birds counted per municipality per year. That is, for each municipality each year, we averaged the number of birds in each report, and then aggregated (summed) the averages of each of the 76 contiguous municipalities per year. Note that this uses municipality as a proxy for locations with an independent population, which is not necessarily the case as birds may fly between municipalities. Violating this assumption could affect our estimates in two ways: overestimating the number of parakeets if counted in two different municipalities during the same year, or underestimating the number of parakeets from the source municipality if not counted there but counted in another municipality. However, because we are averaging per year per municipality, we understand that these effects are negligible.

### Range expansion of the White-winged Parakeets

To assess the range expansion of White-winged Parakeets in Puerto Rico, we used historical occurrence locations derived from the literature and eBird used by Falcón and Tremblay (2018). Due to lack of information on the home ranges of White-winged Parakeets (or *Brotogeris* parakeets in general), we assume an area of 1.5 $km^2$ to be their home range, which is larger than the home range recorded for other parakeet species (e.g., Robinet and Salas 1999, Strubbe and Matthysen 2011). We considered, chronologically, each point as the center of the parakeets' range and assumed a 2.5 $km^2$ buffer around it (we added one squared kilometer to the assumed home range to avoid counting individuals from the same population in adjacent locations). By doing so, all points that fell in the buffer were treated as the same record location, even if these were observations from different years (i.e., once the area is occupied, there cannot be range expansion into the same area). Consequently, we ended up with a dataset that was comprised of the total range per year, allowing us to visualize and calculate range expansion (independent locations per year multiplied by the assumed home range). Because we added a 67% increase to the assumed home range of the parakeets to calculate range expansion, our analysis and parameter estimates should be considered conservative.

### Diet and nesting ecology of the White-winged Parakeet

During the study period, we made observations on the nesting ecology and diet of the White-winged Parakeet in the Metropolitan Area of San Juan. Observations for breeding and nesting activity were made year-round for the first year of this study (2007) and were later concentrated during the months of December–June for each subsequent year because the nesting season corresponded with that reported in the invasive range of Florida and in southwest Puerto Rico (Tossas *et al.* 2012, Brightsmith *et al.* 2017). Diet observations were made opportunistically upon encountering flocks, in addition to data used from Pérez-Rivera *et al.* (1984).

### Statistical analyses

We performed all data pre-processing, obtained summary statistics, and visualizations using R ver. 3.3.3 (R Core Team 2017), and package *ggplot2* for producing figures (Wickham 2016). We mapped occurrence records and visualized distribution results using QGIS ver. 2.18.14-Las Palmas de G.C. (QGIS Development Team 2017).

## Results

### Population ecology of the White-winged Parakeet

We tested the effectiveness of our roost count method by conducting three counts spaced a week apart from September to October 2007 in the San Patricio population, and the population estimates exhibited low variability with a mean of 1,247 birds (counts: 1,164, 1,299, and 1,277 ± 72 SD). The San Germán population of White-winged Parakeets increased from 1,503 birds in 2007 to 3,010 birds in 2010. Although the San Patricio population steadily increased from 1,299 to 3,128 individuals between 2007–2009, a population decline to 2,531 individuals occurred in 2010 (Fig. 1). Both populations exhibited overall positive population growth rates, with a geometric mean $\lambda = 1.24$ (± 0.48) in San Patricio, and $\lambda = 1.26$ (± 0.08) in San Germán during the study period (Table 1). If we consider the population estimates prior to our study (a period of 29 yr in San Patricio and 35 yr in San Germán; Table 1), the populations exhibited λ's of 1.20 (± 0.42 SD) and 1.13 (± 0.13 SD), respectively. Moreover, the island-wide sum of the mean counts per municipality (sighting trends) shows the same pattern of increase (Fig. 1).

Based on the breeding census, we estimated that 40% of the population at San Patricio (625 pairs) and 42% of the population at San Germán (512 pairs) were breeding (Table 2). Based on the number of birds returning to the roost after the breeding season, the number of fledglings (recruitment) was estimated at 604 for San Germán (assuming 2 chicks per pair), but because of the population decline, it was not possible to estimate this for the San Patricio population.

**Range expansion of the White-winged Parakeet**

As with the population and sighting trends, range expansion exhibited a lag-phase with a subsequent exponential increase (Fig. 2). The lag-phase took place between ca. 1985–2005, followed by an exponential increase in 2005–2017.

**Nesting and diet ecology of the White-winged Parakeet**

Although there were tree cavities likely suitable for the White-winged Parakeets in some places where nesting occurred, all recorded nests were constructed in termite mounds of *Nasutitermes* sp. in native and exotic trees (Appendix 1). Two nests inspected with a pipe inspection camera early in the breeding season revealed one clutch of three eggs and one clutch of four eggs. Moreover, five nests inspected later in the breeding season with the same method revealed a mean of 2.14 (± 0.69 SD) chicks per nest.

White-winged Parakeets use mostly exotic species of plants as food resources, and as in their native range, they are primarily frugivorous, but also consume flowers, seeds, and sap (Appendix 1; complimented with data from Pérez-Rivera *et al.* 1984).

68% of species used as food resources were non-native plants and 32% were native, 67% of the species used for nesting resources were non-native plants whereas 33% were native, and of four plant species used as roosting resources, two were non-native and two were native.

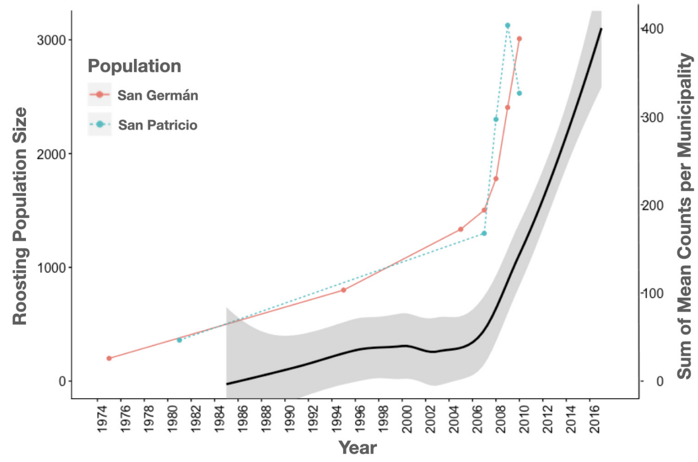


**Fig. 1.** Island-wide sighting trends increase of the White-winged Parakeet (*Brotogeris versicolurus*) in Puerto Rico (black line) and population increase in two roosting sites (red and blue lines) over the years. Island-wide sighting trends increase was calculated as the sum of the mean number of birds counted per year/municipality (data from eBird 2021). Grey shading indicates the 95% CI based on the local weighted scatterplot smoothing (loess).

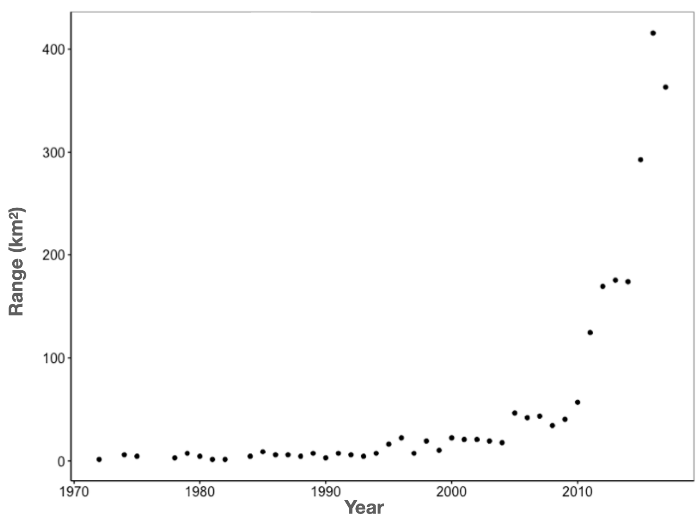


**Fig. 2.** Island-wide geographic range expansion of the White-winged Parakeet (*Brotogeris versicolurus*) in Puerto Rico over the years. Island-wide range expansion increase was calculated using sighting data from eBird (see Methods)..

## Discussion

In this study, we estimated the size of two populations of White-winged Parakeets in Puerto Rico, and assessed their population growth rates, range expansion, and breeding and diet ecology. Moreover, we compared the population dynamics of these two populations of White-winged Parakeets with historic data and sighting trends across the island. Overall, we found that (i) the populations of White-winged Parakeets showed a sustained population increase over the study period, (ii) the populations exhibited extremely high population growth rates, (iii) there was a sustained range expansion, (iv) the species mainly use termite mounds for nesting, (v) the breeding phenology of the population in the Metropolitan Area of San Juan corresponds with that of the population in San Patricio and populations in Florida, and (vi) they have a wide diet breadth but rely heavily on exotic species.

Our population size estimate yields results of positive growth rate and our breeding censuses showed that ca. 40% of the population was breeding, which is consistent with findings for the San Germán population between 2005–2006 (Tossas *et al.* 2012). Comparisons of historic parakeet populations and their

**Table 1.** Population estimates and growth rates (λ) of the White-winged Parakeet (*Brotogeris versicolurus*) at two roosting sites in Puerto Rico. Counts performed in this study (2007–2010, in bold) were conducted during the non-breeding season ($N_{nb}$).

| | San Patricio | | San Germán | |
|---|---|---|---|---|
| **Year** | $N_{nb}$ | λ | $N_{nb}$ | λ |
| 1975 | – | – | 200[A] | – |
| 1981 | 360[A] | – | – | – |
| 1995 | – | – | 800[B] | 1.07 |
| 2005 | – | – | 1,335[C] | 1.05 |
| 2006 | – | – | 1,529[C] | 1.15 |
| **2007** | **1,299** | 1.05 | **1,503** | 0.98 |
| **2008** | **2,301** | **1.77** | **1,779** | **1.18** |
| **2009** | **3,128** | **1.36** | **2,406** | **1.35** |
| **2010** | **2,531** | **0.81** | **3,010** | **1.25** |

[A]Data from Pérez-Rivera *et al.* 1984; [B]from Camacho-Rodríguez *et al.* 1995; [C]from Tossas *et al.* 2012.

**Table 2.** Breeding proportion of the White-winged Parakeet population at two roosting sites in Puerto Rico based on the 2010 breeding ($N_b$) and non-breeding season counts at the roosting site, the estimated number of pairs, expected chick production, and the estimated number of fledglings.

| Population | $N_b$ | Breeding | Pairs | Chicks | Fledglings |
|---|---|---|---|---|---|
| San Patricio | 1,879 | 0.40 | 625 | 1,250 | 604 |
| San Germán | 1,382 | 0.42 | 512 | 1,024 | – |

growth rates with data from this study suggest that the population exhibited a lag-phase and was growing exponentially by 2010. This is consistent with the data on sighting trends obtained from Falcón and Tremblay (2018), and range expansion data (this study; Fig. 2).

One apparent population decrease (2% reduction) occurred in the San Germán population between 2006–2007 (based on data from Tossas *et al.* 2012, and this study), and one population decrease (21% reduction) occurred in the San Patricio population during the study period (2009–2010). The San Germán population had a population growth rate (λ) of 1.15 between 2005–2006 (Tossas *et al.* 2012) and, based on this, was expected to grow from 1,529 to 1,758 parakeets in 2007. However, the following year (2007) we counted only 1,503 parakeets at the San Germán roosting site. Disease, emigration, extreme weather events, or capture may have caused this decline (capturing parakeets is legal in Puerto Rico with a permit from the Department of Natural and Environmental Resources). However, we are unaware of any of these instances occurring in San Germán and no extreme weather events (i.e., direct hurricane hits) happened during this period. Therefore, the apparent population decline in the San Germán population remains unexplained. However, the resulting population decrease in 2010 in San Patricio was probably due to emigration and the establishment of a new roosting site in the Río Piedras Botanical Garden (5.6 km from the San Patricio roosting site), where parakeets were previously observed foraging, but did not roost prior to this splitting event. In August 2010, around 800 parakeets were seen roosting at this new location. If we assume that the parakeets at the new roosting site originated from the San Patricio population, then a minimum of 200 fledglings were produced (considerably lower than the production in San Germán), and about 300 pairs abandoned the San Patricio roost. Another roosting site was established in 2012 at the University of Puerto Rico, 5.5 km from the San Patricio roosting site, and 1.5 km from the Botanical Garden population.

Migration to and from the roosting sites may be a factor that can affect our population growth estimates and bias our results since we are not considering migration and we assume that the changes in populations are due to birth and death rates. Our surveys in the vicinity of both study populations suggested that they were the only existing roosting sites in the areas, a fact that was confirmed by Tossas *et al.* (2012) for the San Germán population. During our surveys, we were able to detect the establishment of a new roosting site, which probably originated from the San Patricio population, so emigration is likely a factor regulating localized population sizes. Although White-winged Parakeets can exhibit yearly variation in terms of the number of individuals at the roost site, the variation is low within the peak of the breeding and non-breeding seasons (Tossas *et al.* 2012). The emigration events of a proportion of the roost to a new site is likely determined by some density threshold cue or resource limitation close to the roosting site.

The roost count method was evaluated along with point transects, line transects, and mark-recapture by Casagrande and Beissinger (1997), and the four methods produced overlapping 95% confidence intervals and similar population estimates. Moreover, we tested this method over a three-week period, and the estimates exhibited very low variability (± 72 SD). However, we assume that there is spatial and temporal consistency within and between the two populations across time, and that there is no difference in observation error between years. For example, counts in San Patricio were performed at dawn and birds were counted as they left the roost, while counts in San Germán were performed at dusk, and birds were counted as they entered the roost. Different temporal activity dynamics between populations and time of day may therefore affect the counts (i.e., flock size variation, period of activity, and detection probability). Since we did not perform the same test each year and only did so for the San Patricio population, it is not possible to determine if these assumptions are violated, which could affect our results by possibly underestimating the number of birds counted. Ideally, roost count method tests should be conducted in each sub-population each year to assess counting error and get more robust estimates. However, it is worth mentioning that Tossas *et al.* (2012) performed monthly counts in the San Germán population, from August 2005 through July 2006 spanning two non-breeding seasons, and noted relatively low variation between months (August–December 2005 ± 12 SD and

May–July 2006 ± 189 SD). Given that we conducted the counts to estimate the population size during the non-breeding season, and that we were able to detect the establishment of the new roosting site, which likely explains the population decline in San Patricio, we are confident that our methods and estimates are representative of the reality in the field.

Population growth rates of bird species regarded as invasive are usually exponential, and often exhibit a lag-phase before the exponential growth phase (Sakai *et al.* 2001, Blackburn *et al.* 2009). We observed both patterns in the Puerto Rican populations of the White-winged Parakeet. Although some species may exhibit very rapid population growth and range expansion, many bird species tend to have long lag-phases between the time of initial introduction and later exponential population growth, e.g., Eurasian Collared-Dove (*Streptopelia decaocto*) (Isenmann 1990), the Eurasian Penduline-Tit (*Remiz pendulinus*), and the European Serin (*Serinus serinus*) (Hengeveld 1989). Three main mechanisms have been proposed to explain the lag-phase often exhibited by invasive species: inherent, environmental, and genetic mechanisms (Crooks and Soulé 1999). The inherent lag effect is the expected lag in population growth of founder populations, whether or not they are adapted to the new environment (e.g., using Equation 1, the population grows relatively slowly in absolute numbers, which is depicted by the shallow portion early in the growth curve; ibidem). Environmental lag effects refer to situations where environmental changes enhance the fitness of the species, and triggering an increase in its growth rate, which would result in a longer lag-phase than that expected from the inherent lag effect (ibidem). Moreover, genetics may cause lag-phases in species as founder populations may lack local genetic adaptations to the abiotic or biotic environment, and a period of time may be needed for new genetic combinations to arise via mating, the appearance and spread of beneficial mutations through the population (ibidem), or the appearance and spread of novel beneficial genotypes as a result of secondary contact between individuals of genetically distinct populations.

Although there is no way of determining which intrinsic or extrinsic variables are most responsible for the population lag-phase of the White-winged Parakeet in Puerto Rico, recognizing that multiple different mechanisms are likely at play, we believe that food and nesting resource limitation may have been a major cause of a slow population increase. In the late 1930s, ca. 90% of the land in Puerto Rico was used for agriculture, and during the 1950s the economy of Puerto Rico began shifting from agriculture to manufacturing, which resulted in the abandonment of many agricultural lands and subsequent development of secondary forests (Grau *et al.* 2003). Today, forest cover (predominantly woody vegetation) is estimated at 53% (Gould *et al.* 2008). As a result, we believe that food and nesting (termite mounds) resources used by the White-winged Parakeet have increased dramatically, which may have aided in the population increase and range expansion.

Exotic species that exhibit high population growth rates may be more likely to establish viable populations (Ehrlich 1986, Moulton and Pimm 1986, Pimm *et al.* 1988, Pimm 1989, Cassey 2001). Additionally, as the size of species' population increases, so does the geographic distribution (Veit 1997), so we can expect that population growth will probably result in spread, but not always (Gaston 2003, Gaston *et al.* 2003, Blackburn *et al.* 2006). It has been proposed that bird populations exhibiting a positive population growth rate have a proportional increase in long dispersing individuals (vagrants) to the increase in population size, thus increasing the chances of the species invading new ranges (Veit 1997, 2000). Our data and observations suggest that the rapid increase and high number of parakeets in the San Patricio population led to the emigration and establishment of new roosts, therefore expanding their range. This is supported by the lag between population increase at the largest roosting sites on the island, and the island-wide population increase (based on sighting trends; Falcón and Tremblay 2018).

The nesting phenology observations in the Metropolitan Area of San Juan are consistent with the findings of the population in San Germán (Tossas *et al.* 2012), and in Florida (Brightsmith *et al.* 2017). Moreover, dietary observation of the White-winged Parakeet corresponds with previous reports on the island (Pérez-Rivera *et al.* 1984), and are consistent with those reported elsewhere in their invasive and native range (Brightsmith *et al.* 2017). It also shows that although the parakeets use native species, most of the plant species consumed in Puerto Rico are exotic. It is worth noting that we recorded White-winged Parakeets feeding on economically important crops such as soursop (*Annona muricata*), papaya (*Carica papaya*), grapefruit (*Citrus paradisi*), Barbados cherry (*Malpighia emarginata*), mango (*Mangifera indica*), and banana (*Musa acuminata*). Although these observations were made mostly in urban areas, we have observed the presence of parakeets, albeit in low densities, near important agricultural areas, such as in the Lajas Valley in the southwest of Puerto Rico. However, we are unaware of any reports indicating negative impacts by White-winged Parakeets on agriculture in Puerto Rico.

Various factors may have contributed to the recent success of White-winged Parakeets in Puerto Rico. Firstly, propagule pressure, the number of individuals of a species released into an area where they are not native (Lockwood *et al.* 2005), may have been an important factor leading to the introduction and establishment during the 1960s and 1980s, when these birds were popular and cheap. According to the CITES Trade Database (2023), the main exporter to the USA (and therefore Puerto Rico) was Peru, with 2,832 White-winged Parakeets exported in a single shipment in 1985. Secondly, they have a wide diet breadth, and make use of common species that are found especially in anthropogenically modified areas, with which this species' distribution is highly associated (Falcón and Tremblay 2018). Thirdly, because they nest in termite mounds, which are highly abundant in the secondary forests of Puerto Rico and urban areas (especially in parks), White-winged Parakeets are not limited by the scarcity of tree cavities as other parrot species. Fourthly, no predation observation have been noted, suggesting that predation pressure is low, and the potential predator pool is rather small (including *Falco peregrinus*, *F. columbarius*, *F. sparverius*, *Accipiter striatus*, and *A. cooperii*; Brightsmith *et al.* 2017). Fifth, trapping seems to supply the local (informal) pet market, rather than serving for exportation, further increasing the parakeet numbers in the wild (Falcón and Tremblay 2018).

Based on their wide distribution across the island and sighting trends compared to other species (Falcón and Tremblay 2018), their positive growth rates, and ability to successfully colonize new areas, White-winged Parakeets can indeed be considered the most successful psittacine species in Puerto Rico. Although concerns have been raised about the possible negative impacts that psittacine species introduced to Puerto Rico may have on endemic and native species (e.g., on the Puerto Rican Parrot, *Amazona vittata*), and on the agricultural sector, we found no reports indicating that White-winged Parakeets are currently having negative impacts (see Tremblay and Falcón 2018 for discussion). Whether such a fast-growing species poses a threat and can cause negative impacts remains to be studied. Finally, the success of this species, as well as their large numbers and distribution, present research opportunities for studying population management with conservation application for parrots and parakeets in their native range.

## Acknowledgments

We want to especially thank Rafael D. Rodríguez, Linda I. Ortíz, and Rebecca Hernández for their help in the field during the White-winged Parakeet roost counts. The PR-Louis Stokes Alliance for Minority Participation Bridge to the Doctorate Fellowship (HRD-0601843), the Ronald E. McNair Program of the University of Puerto Rico at Humacao (P217A070213), and the Center for Applied Tropical Ecology and Conservation (HRD-0734826) provided funding to WF in partial support of this project. Author Contributions: WF conceived the project, WF and RT developed the methodologies, WF, RT and volunteers gathered field data, WF gathered data from online sources and the literature, WF and RT analyzed the data and wrote the manuscript.

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**Appendix 1.** Plant resources used by the White-winged Parakeet (*Brotogeris versicolurus*) for food and nesting in Puerto Rico. Information based on observations made during the study period, with additional information from Pérez-Rivera *et al.* (1984).

| Species | Common Name | Status | Resource Used |
|---|---|---|---|
| Food Resources | | | |
| *Albizia procera* | White siris | Invasive | Sap |
| *Annona muricata* | Soursop | Exotic | Fruits |
| *Artocarpus heterophyllus* | Jackfruit | Exotic | Flowers |
| *Bucida buceras* | Bullet tree | Native | Flowers, seeds |
| *Callistemon citrinus* | Lemon bottlebrush | Exotic | Flowers, nectar |
| *Carica papaya* | Papaya | Exotic | Fruits |
| *Cassia javanica* | Pink shower tree | Exotic | Flowers |
| *Cassuarina equisetifolia* | Australian 'pine' | Invasive | Seeds |
| *Cecropia peltata* | Trumpet tree | Native | Fruits |
| *Ceiba pentandra* | Kapok | Native | Flowers |
| *Citrus paradisi* | Grapefruit | Exotic | Fruits |
| *Clusia rosea* | Autograph tree | Native | Seeds |
| *Cocos nucifera* | Coconut palm tree | Exotic | Flowers, nectar? |
| *Cordia sebestena* | Scarlet cordia | Native | Flowers, nectar? |
| *Delonix regia* | Royal poinciana | Exotic | Flowers |
| *Erythrina poeppigiana* | Coral tree | Exotic | Shoots |
| *Ficus americana* | West Indian fig | Native | Fruits |
| *Ficus citrifolia* | Shortleaf fig | Native | Fruits |
| *Inga vera* | Guaba | Native | Seeds |
| *Malpighia emarginata* | Barbados cherry | Native | Fruits |
| *Mangifera indica* | Mango | Exotic | Flowers, fruits |
| *Musa acuminata* | Banana | Exotic | Fruits |
| *Musa paradisiaca* | Plantain | Exotic | Fruits |
| *Ochroma pyramidale* | Balsa | Exotic | Seeds |
| *Pithecellobium dulce* | Manilla tamarind | Exotic | Flowers, seeds |
| *Psidium guajava* | Guava | Exotic | Fruits |
| *Pterocarpus officinalis* | Dragonsblood tree | Native | Flowers |
| *Roystonea borinquena* | Royal palm | Native | Fruits |
| *Spathodea campanulata* | African tulip tree | Exotic | Flowers, seeds |
| *Spondias mombin* | Yellow mombin | Exotic | Fruits |
| *Spondias purpurea* | Red mombin | Exotic | Fruits |
| *Sterculia apetala* | Panama tree | Exotic | Seeds |
| *Swietenia mahogani* | West Indian mahogany | Exotic | Seeds |
| *Syzygium jambos* | Water apple | Exotic | Fruits |
| *Tabebuia heterophylla* | Pink trumpet tree | Native | Flowers, seeds |
| *Terminalia catappa* | Indian almond | Exotic | Fruits |
| *Zanthoxylum martinicense* | Prickly ash | Native | Shoots |

**Appendix 1.** cont.

| Species | Common Name | Status | Resource Used |
|---|---|---|---|
| Roosting Resources | | | |
| *Calophyllum antillanum* | Antilles calophyllum | Native | – |
| *Roystonea sp.* | Royal palm | Unknown | – |
| *Eucalyptus deglupta* | Rainbow eucalyptus | Exotic | – |
| *Swietenia mahogani* | West Indian mahogany | Exotic | – |
| Nesting Resources | | | |
| *Albizia procera* | White siris | Invasive | Termite mounds |
| *Artocarpus heterophyllus* | Jackfruit | Exotic | Termite mounds |
| *Cordia sulcata* | White manjack | Native | Termite mounds |
| *Delonix regia* | Royal poinciana | Exotic | Termite mounds |
| *Dendropanax arboreus* | Angelica tree | Native | Termite mounds |
| *Ficus citrifolia* | Shortleaf fig | Native | Termite mounds |
| *Mangifera indica* | Mango | Exotic | Termite mounds |
| *Pithecellobium saman* | Albizia saman | Exotic | Termite mounds |
| *Schefflera morototoni* | Yagrumo macho | Native | Termite mounds |
| *Spondias mombin* | Yellow mombin | Exotic | Termite mounds |
| *Swietenia macrophylla* | Honduran mahogany | Exotic | Termite mounds |
| *Swietenia mahogani* | West Indian mahogany | Exotic | Termite mounds |
| *Tamarindus indica* | Tamarind | Exotic | Termite mounds |
| *Terminalia catappa* | Indian almond | Exotic | Termite mounds |
| *Zanthoxylum martinicense* | Prickly ash | Native | Termite mounds |