Interactions between non-native parrot species and their recipient environments

PhD Thesis

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Interacciones entre especies de psitácidos exóticos y los nuevos medios que ocupan

Thesis for the degree of Doctor

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Que no puede ser sino salvaje y desmedido

Jean-Claude Nicolas Forestier

Arquitecto paisajista

(Durante el diseño del Parque de María Luisa)

A mis padres

CONTENT

SUMMARY

Biological invasions are amongst critical causes of biodiversity loss around the world, although interactions between invasive species, native biota and recipient environment are mostly unknown. Their identification may show how certain invasive species are able to establish successfully in novel environments and which potential ecological impacts threaten native biota. However, both interactions and their potential impacts are usually overlooked, especially in first stages of invasion, because they may arise between unexpected interact species as well as their detection depends of long-term studies. Parrots (Order Psittaciformes) are one of the groups most affected by international wildlife trade due to their appraisal as pets, consequently, 16% of parrot species present populations established out of their native range. Between non-native parrots, rose-ringed (*Psittacula krameri*) and monk (*Myiopsitta monachus*) parakeets are the most successful to establish and invade novel environments, even though numerous introductions have occurred in more than forty countries worldwide, their biotic interactions and impacts are poorly known. In this thesis, we combine different observations (behavioral, spatial distribution, environmental and population) to assess the role of different biotic interactions and their resultant impacts that arise between a several non-native parrot species (mainly rose-ringed and monk parakeets), recipient environment and biota. Our results show that non-native parrot species develop a wide range of biotic interactions (e.g. interspecific competition for nesting sites, facilitation of limiting resources and animal-plant mutualisms) that may threaten or benefit several coexisting species, both native and non-native. Thus, the emergence of adaptive behaviors (e.g. nesting association and innovation) in non-native parrots allows for overcoming barriers from recipient environment, such as biotic resistance and scarcity of limiting resources, or obstacles during their first stages of establishment (e.g. Allee effects). Overall, the wide analysis and study in long-term of biotic interactions here performed shows their importance as one of key mechanisms for success of establishment and invasion process in non-native parrots species. Moreover, their associated ecological impacts are a risk for native species, especially threaten species, hence, the implementation of efficient management plans is urgently necessary to conserve the biodiversity.

Key words: *Psittaciformes; biological invasions; interspecific competition; biotic resistance; commensalism; behavioral innovation; facilitation; hybridization; Allee effect; animal-plant mutualism; seed dispersal; zoochory; impact; eradication; management plans; population viability*

RESÚMEN

Las invasiones biológicas están entre las causas más importantes de pérdida de biodiversidad en todo el mundo, aunque las interacciones entre las especies invasoras, la biota nativa y el medio receptor son en su mayoría desconocidas. Su identificación puede mostrar cómo ciertas especies invasoras pueden establecerse exitosamente en nuevos ambientes y qué impactos ecológicos potenciales amenazan la biota nativa. Sin embargo, tanto las interacciones como sus impactos potenciales generalmente se pasan por alto, especialmente en las primeras etapas de la invasión, porque éstos pueden surgir entre especies que interactúan inesperadamente, por lo que su detección depende de estudios a largo plazo. Los loros (Orden Psittaciformes) son uno de los grupos más afectados por el comercio internacional de vida silvestre debido a su valor como mascotas, por lo que el 16% de las especies de loros presentan poblaciones establecidas fuera de su área de distribución nativa. Entre los loros no nativos, las cotorras de Kramer (*Psittacula krameri*) y argentina (*Myiopsitta monachus*) son las más exitosas para establecerse e invadir en nuevos ambientes, aunque se han producido numerosas introducciones en más de cuarenta países de todo el mundo, sus interacciones e impactos bióticos son poco conocidos. En esta tesis, combinamos diferentes observaciones (conductuales, de distribución espacial, ambientales y poblacionales) para evaluar el papel de las diferentes interacciones bióticas y sus impactos resultantes que surgen entre diferentes especies de loros no nativos (principalmente cotorras de Kramer y argentina), ambiente y biota receptores. Nuestros resultados muestran que las especies de loros no nativos desarrollan una amplia gama de interacciones bióticas (por ejemplo, competencia interespecífica por sitios de anidación, facilitación de recursos limitantes y mutualismos animal-planta) que pueden amenazar o beneficiar a varias especies coexistentes, tanto nativas como no nativas. Por lo tanto, la aparición de comportamientos adaptativos (por ejemplo, asociación e innovación en la anidación) en loros no nativos permite superar las barreras provenientes del ambiente receptor, como la resistencia biótica y la escasez de recursos limitantes, u otros obstáculos durante sus primeras etapas de establecimiento (por ejemplo, efectos Allee). En general, el amplio análisis y estudio a largo plazo de las interacciones bióticas aquí realizado muestran su importancia como uno de los mecanismos clave para el éxito del proceso de establecimiento e invasión en especies de loros no nativos. Además, sus impactos ecológicos resultantes son un riesgo para las especies nativas, especialmente las especies amenazadas, por lo que la implementación de planes de manejo eficientes es urgente para conservar la biodiversidad.

Palabras clave: *Psittaciformes; invasiones biológicas; competencia interespecífica; resistencia biótica; comensalismo; innovación comportamental; facilitación; hibridación; Efecto Allee; mutualismo planta-animal; dispersión de semillas; zoocoria; impacto; erradicación; planes de manejo; viabilidad poblacional*

THESIS INTRODUCTION

Biological invasions: an issue for global biodiversity

Biodiversity is resultant of natural history processes that operate in different space-time scales and influence on key factors from genetic, through species and environmental to ecologic by which assemble the biological heterogeneity (Walker 1992). Likewise, biodiversity influences on ecosystem functions and provides good and services to humanity (Cardinale et al. 2012). However, the disruption of human activity has driven deep alterations on these processes and consequently endanger the local and global biodiversity (Vitousek et al. 1997; Cardinale et al. 2012). In this sense, the increasing biodiversity loss and extinction rates during the last century are unprecedented in previous geological ages, resembling thus massive extinctions from fossil record evidences (Dirzo et al. 2014; Ceballos et al. 2015; Wilson 2016). Such human impact acceleration on biodiversity compromises its understanding and detection of its causes and consequences, which in its turn spoil efforts to preserve global biodiversity (Dawson et al. 2011). Thus, different disruptive human actions are the most important drivers of biodiversity loss such as habitat destruction, overexploitation, climate change and biological invasions (Sala et al. 2000; Williams et al. 2008), as well synergetic interactions between these drivers may increase further their impacts (Mantyka-pringle et al. 2012).

Translocation of animal and plants by humans have occurred during different human migrations worldwide. Pimentel (2001) estimates that about 400,000 species have been removed from their natural geographical areas to another by human agency during the past 10,000 years. Although there is a considerable increasing in translocation rates since 18th century due to technological advances that have assisted the long-distance transport (Meyerson and Mooney 2007; Hulme 2009). By deliberately or accidentally transporting, a large number of species have been introduced in novel environments, whereby these species have overcome geographical barriers and established non-native viable populations out of their native ranges (Blackburn et al. 2011; Seebens et al. 2017). The establishment and spread of these non-native species (i.e. biological invasion process) may involve impacts on native species, community dynamics and ecosystem functions (Clavero and García-Berthou 2005; Vilà et al. 2011), in addition to economic damages and health issues (Vitousek et al. 1996; Simberloff et al. 2013). Native species may be affected through negative impacts such as predation, competition, spread of diseases and hybridization (Mack et al. 2000; Money and Cleland 2001), hence, their consequences threat viability of native populations, even their extinction (Clavero et al . 2009; Bellard et al. 2016).

Nevertheless, the role of factors that drive processes in which non-native species become invasive, establishing and spreading successfully in new geographical areas, it has been debatable among numerous hypotheses (Kolar and Lodge 2001; Catford et al. 2009; Blackburn et al. 2011). Overall, these key factors are mainly categorized in three groups that may show synergy between them and change their relevance regarding a specific stage of invasion process (i.e transport, introduction, establishment and spread) (Kolar and Lodge 2001; Duncan et al. 2003; Blackburn et al. 2011; Abellán et al. 2017). First, event-level factors regarding the number of introductions and individuals released across the invasion history (i.e propagule pressure) (Lockwood et al. 2005). Second, location-level factors attributed to recipient environment traits such as coexisting native species similar to non-native species and climate matching regarding their native ranges (Forsyth et al. 2004; Cardador et al. 2016). Third, species-level factors or advantageous traits that show non-native species such as high abundances range-wide of their natural distribution, fast demographic growth rates and behavioral flexibility (Sol et al. 2005; Blackburn et al. 2009; van Kleunen et al. 2010).

Whereas several biotic traits are considered in the understanding of biological invasion success, mechanisms of biotic interactions are relegated of impact studies on native communities, despite of their importance in shaping species distributions (Wisz et al. 2013). Both direct and indirect biotic interactions between non-native species and recipient communities are expected during different stages of invasion process, although it is widely unexplored their influence on success of establishment and spread of non-native species (Catford et al. 2009), especially in vertebrates (Blackburn et al. 2011).

Novel interactions between non-native species and recipient communities

After their introduction in novel environments, non-native species may gain or lose biotic interactions in relation to interactions that are previously present in their natural distribution ranges (Catford et al. 2009). These interactions may influence on non-native and native populations, so they are also keys determinating the success or failure of establishment and invasion processes, both through the loss (e.g. Enemy Release and Missed Mutualisms Hypotheses; (Elton 1958; Alpert 2006)) and gain of interactions (e.g. Invasional Meltdown and Biotic Resistance Hypotheses; (Elton 1958; Simberloff and Von Holle 1999)). Moreover, non-native species are mostly generalist (Wolf et al. 1996; Cassey et al. 2004; Sol et al. 2005), hence, the emergence of novel interactions to replace generalist interactions may occur more rapidly than those which are restrictive such as specialist (Traveset and Richardson 2014). As examples of how novel interactions works both ways, on the one hand, recipient community may display biotic barriers for invasive species such as a high diversity of natural enemies (e.g. predators and competitors) that produce biotic resistance against invasion process (Vilà and Weiner 2004; de Rivera et al. 2005; Foelker et al. 2018). On the other hand, coexisting invasive species may develop beneficial interactions between them, facilitating thus their invasion process as well as their impacts on native community through invasional meltdown processes (Adams et al. 2003; Johnson et al. 2009). All these interactions usually categorize regarding their effect on each interacting species, namely negative, positive and neutral interactions. (Simberloff and Von Holle 1999). Most studies about biotic interactions and associated ecological impacts on native species focus on negative facets such as predation, competition and parasitism (Blackburn et al. 2009; Clavero et al. 2009; Ruscoe et al. 2011). However, positive interactions, such as facilitation, may also develop between native and invasive species and benefit both species, although few studies have tested their population effects and invasion success (Richardson et al. 2000; Altieri 2010; Wright et al. 2016) and only recorded in plants and invertebrates.

Biotic interactions play a role between different ecological hypotheses aimed at explaining biological invasions although a correct assessment of impacts on native communities may be challenging, chiefly overlooked impacts and long-term ecological effects (Strayer et al. 2006; Simberloff et al. 2013; Blackburn et al. 2014). Thus, it is essential the implementation of a holistic approach that displays the complexity of ecological interaction networks and that includes biotic interactions from invasive species and as well as life-history traits of invaders and recipient communities (Catford et al. 2009). Besides, the role of biotic interactions may hide due to other key factors if the focus is wrong depending on in which stage of invassion process is working (Abellán et al. 2017). Therefore, this holistic approach may be fundamental to predict impacts on native biota and environment, developing thus effective management plans against biological invasions.

Parrots, unintentional characters in the scenario of biological invasion

A wide variety of animal groups are removed from their native geographic ranges due to the international wildlife trade (Beissinger 2001; Oldfield 2003; Young et al. 2016), a lucrative business but an ecological disaster that is an introduction pathway for several non-native species whereby they establish in novel areas after their release (Carrete and Tella 2008; Reino et al. 2017). Among birds, parrots (Order: Psittaciformes) are one of the groups most affected by wildlife international traffic with millions of individuals traded only a decade ago, ergo, 73% of 355 living parrot species have been traded (Beissinger 2001; Romero-Vidal et al. 2020). Some activities employed during the removal of parrots from their natural areas (e.g. poaching and transport) are associated a high mortality rates among captured individuals (Wright et al. 2001). Thus, trade and together with habitat loss are main threat causes for one third of total living parrot species (Donald et al. 2010; Olah et al. 2016). Since ancient times, parrots have awaken interest between different human groups (Tella 2011) and nowadays they are greatly appreciated as exotic pets because show attractive traits for pet owners such as colorful plumage and abilities to imitate human speech (Tella and Hiraldo 2014). However, accidental or deliberate releases from captivity are the origin of non-native parrot populations, consequently, 16.6% of total parrot species (over 60 species) show populations established worldwide out their native range (Cassey et al. 2004; Menchetti and Mori 2014; Cardador et al. 2017), including invasive species.

Despite this high incidence rate of removed parrots from their natural areas as well as that they are an old and highly diversified group, not all traded species show non-native populations. Non-native parrot species show different importation rates that produce biases on the proportion of removed and transported individuals (Cassey et al. 2004), so the establishment success positively depends of number of introduction events and individuals released (i.e. propagule pressure) (Duncan et al. 2003; Abellán et al. 2017). Likewise, life-history traits affect directly on colonization of novel environments and non-native parrot species mostly share some suitable traits such as small-medium sizes, broad diets, generalist for environmental conditions, and synanthrope (Cassey et al. 2004). Moreover, behavioral flexibility shown by parrots as response to environmental changes on limiting resources (e.g. food and nest sites) is also considered as a key species trait in the successful establishment of non-native populations (Lefebvre et al. 2004; Renton et al. 2015). Consequently, this combination of factors causes that highest diversities and abundances of non-native parrot species are mostly introduced in urbanized areas owing to a greater likelihood of releases compared to rural and natural areas (Abellán et al. 2017). Furthermore, urban environments provide non-native parrots several advantages to establish self-sustainable populations, such as a predation pressure attenuation, lesser disruptive human actions (e.g. poaching) and abundant food sources from coexisting non-native plants (Davis et al. 2011; Rebolo-Ifrán et al. 2017). This combination of factors could not only facilitate the establishment and spread of non-native parrot species, but also the detection and identification their biotic interactions and associated impacts regarding native community and recipient environment, however, they are overlooked and poorly documented in the literature (Menchetti and Mori 2014; White et al. 2019).

This lack of knowledge is especially remarkable if it is considered available information about biotic interactions in their native geographic areas, to predict them in their introduced ranges and assess their effects on non-native parrot populations (de Araújo et al. 2014; Renton et al. 2015). For instance, parrots are generally secondary cavity nesters (Renton et al. 2015) and depend availability of cavities in environment to nest successfully, so parrots usually display territorial behavior and aggressions, both interspecific and conspecific, against nesting competitors during breeding season (Renton et al. 2015). Thus, it should expect that a potential competence for nesting sites between non-native parrots and native cavity nesters in their introduced areas.

Regarding potential interactions between parrots and plant community, parrots are generalists herbivores that exploit a high diversity of plant species and different parts such as, fruits, flowers and seeds (Renton et al. 2015; Toft and Wright 2015). Although, parrots are widely considered as seed predators, their foraging behaviors also provide some mutualistic interactions (i.e. seed dispersals) with plant community (Blanco et al. 2018, 2020; Tella et al. 2015, 2020) and ecological functions (Blanco et al. 2015; Montesinos-Navarro et al. 2017) that have been largely overlooked. Mostly, recorded impacts from foraging activity of non-native parrots are involded in crop damages (Menchetti and Mori 2014; White et al. 2019), being not unusual if a considerable number of parrots species are considered as pests in several countries from their natural geographical distribution (Lever 2005). Contrary, potential animal-plant interactions and their role as mutualist in the scenario of biological invasions are poorly documented (Runde et al. 2007; Thabethe et al. 2015). Therefore, these potential interactions may affect indirectly on other coexisting species and ecological functions that trigger cascading effects with unexpected consequences (Blanco et al. 2018) or synergetic interactions between non-native species (Ancillotto et al. 2016) that accelerate the emergence of impacts on native communities and recipient environments.

Study species: the most successful invaders and other non-native parrot species

Among introduced parrot species worldwide, the rose-ringed parakeet (*Psittacula krameri*) and the monk parakeet (*Myiopsitta monachus*) are one of most successful and widespread invasive birds (Lever 2005). Rose-ringed and monk parakeets are naturally distributed in Central Africa-South Asia and southern South America respectively (Forshaw 2010), in addition, both show non-native populations in 39 and 19 countries respectively, on five continents and some oceanic islands (Lever 2005; Edelaar et al. 2015; Pârâu et al. 2016). Millions of wild-caught individuals of both parakeet species have been removed from their native areas for decades (Carrete and Tella 2008; Strubbe and Matthysen 2009a), becoming thus in popular pets during last decades, so first records of successful establishment in their introduced ranges are from late 1960s and early 1970s (Butler 2005). Both parakeet species share similar traits, such as medium body sizes, broad diets, gregarious behavior, and wide environmental tolerances that assist their invasion processes (Cassey et al. 2004). Although their main differences are in relation to nesting behaviors, while rose-ringed parakeet is a secondary cavity nester that breeds mainly in tree cavities as the majority of parrot species (Renton et al. 2015), monk parakeet is the only parrot species that builds their own nests with wood sticks and that locate on trees or human facilities (Senar et al. 2019).

Concerning their status as avian invaders, both parakeet species are categorized as invasive species for a wide number of recipient countries, for instance, rose-ringed parakeet is considered as amongst the 100 worst invasive species in Europe (DAISIE 2008), although their impacts on native communities are barely known. The scarce information about recorded impacts from both species is mainly focused on damage assessments on crops (Stafford 2003; Fletcher and Askew 2007; Senar et al. 2016; Postigo et al. 2017) and infrastructures (Avery et al. 2002), as well few evidences about competition with cavity nester species (Strubbe and Matthysen 2009b; Strubbe et al. 2010; Yosef et al. 2016), competition for food resources (Freeland 1973; Peck et al. 2014), and vectors of diseases and parasites (Fletcher and Askew 2007; Runde et al. 2007; Mori et al. 2015; Briceño et al. 2017; Ancilloto et al. 2018; Morinha et al. 2020). Besides, it is unknown the role of biotic interactions in the establishment success of both species, in which, previous studies have focused in other key factors, such as event- level (propagule pressure), climate-matching and phenological (Strubbe and

Matthysen 2009a; Jackson et al. 2015; Cardador et al. 2016; Abellán et al. 2017; Luna et al. 2017).

To this day, the most of available information about impacts and biotic interactions of non-native parrot species is focused both rose-ringed and monk parakeets (Menchetti and Mori 2014; White et al. 2019). Nevertheless, other non-native parrot species are introduced in noteworthy numbers worldwide (e.g. genera *Amazona*, *Brotogeris*, *Nandayus*, and *Poicephalus*) (Abellan et al. 2016; Cardador et al. 2017) and it is still unknown their population status, biotic interactions and impacts on native biota (Mori et al. 2017; White et al. 2019), due to their populations are mostly small so further complicating their detection. Additionally, these populations are usually in early stages of introduction and establishment processes (Cassey et al. 2004) as well as non-native parrot populations frequently show lag periods that disrupt their population growth (Runde et al. 2007), especially in species with slow reproduction rates, hence, their interactions with native community and recipient environment may be ignored for years (Blackburn et al. 2014). However, potential impacts could be similar to observed in rose-ringed and monk parakeets, as crop damages and competence for nesting resources, that have been also recorded in their native ranges (Runde et al. 2007; Mori et al. 2017).

Due to the aforementioned series of potential and recorded impacts, management plans are necessary to resolve associated problems from irruption of non-native parrots in their occupied areas. Although international and local bans focused on non-native and invasive parrot species have considerably limited their legal trade and possession, hence, the invasion risk (Cardador et al. 2019), it is not sufficient to address issues from self-sustainable populations already well established for years and showing growing populations (Pârâu et al. 2016; Postigo et al. 2017). However, the same attractiveness of parrots that arouses between pet owners may also show on rest of citizens and consequently, do not support control or eradication plans on non-native parrots despite the legal coverage of these actions (Crowley et al. 2019). Thus, most management plans focused on non-native parrots have failed due to low social support (Van Bael and Pruett-Jones 1996; Avery and Tillman 2005) and ineffective methods (Pruett-Jones et al. 2007; Avery et al. 2008; Avery and Shiels 2018), contrary those successful actions focused on some rose-ringed and monk parakeet populations (Esteban 2016; SIF 2017; Bunbury et al. 2019; Saavedra and Medina 2020). Therefore, the success of management plans against non-native populations does not only depend of social support through awareness campaigns (Blackburn et al. 2010), but also the implementation of feasible and efficient actions, especially in early steps of invasion (Edelaar and Tella 2012).

Objectives, hypotheses and thesis structure

Overall, we hypothesize that biotic interactions performed by non-native parrot species in novel environments may be exhibited in response to dynamics and evolutionary components that equally may loss or gain during the introduction process and, consequently, may effect on native biota. Thus, this doctoral thesis explores potential biotic interactions between non-native parrot species, recipient environment and native biota, to fill gaps in knowledge of biotic interactions in biological invasions. Besides, it aims to detect and understand their role as key mechanisms that determinate the success of establishment and invasion processes of study non-native parrot species (invasiveness) as well as their associated impacts on native biota. In order to assess their importance, we focus on negative and positive interactions between two different invasive parrot species and recipient cavity nester community and that may induce impacts on native fauna (**Section 1**). We also combined different novel adaptive interactions showed by several non-native parrot species to infer how limitations from recipient environment may trigger behavioral innovations and strategies to avoid them, favoring thus the invasion process (**Section 2**). We focus on animal-plant mutualism in which non-native parrots species interact with recipient vegetal community and their potential effects on native flora (**Section 3**). Finally, we assess the feasibility and efficiency of a hypothetical management plan focused on an invasive parrot species (**Section 4**).

This doctoral thesis is constituted by four sections that describe the framework, justification, specific hypotheses and predictions of main goals. Different analytical approaches have been used in each section, material and methods in this thesis are described in detail within each section.

In the **Section 1**, we monitored an invasive population of rose-ringed parakeet in an urban park located in Seville, Spain, to test potential interspecific competition for nesting sites (tree cavities) between the cavity nester community. Besides, we censuded several monk parakeet populations in different invaded areas to assess its potential facilitation of nesting sites for coexisting cavity nester species. We address particular questions such as (i) whether rose-ringed parakeet exploits nesting resources unexploited by natives (opportunism hypothesis) or it may share same preferences to exploit resources outcompeting aggressively with the rest of cavity nesters (competition hypothesis) (Sol et al. 2012), (ii) how the distribution of rose-ringed parakeet nests and their interspecific aggressions influence on spatial nesting distribution of rest of cavity nesters, (iii) whether a coexisting threatened bat species, the greater noctule (Alcalde et al. 2016), is more sensitive to competition pressure or both species do not interaction as well as what impacts emerge on its population during a time window of 14 years regarding the growing rose-ringed parakeet population, (iv) whether monk parakeet also facilitates alternative nesting sites with own built nests to several species in its invasive range, and (v) how tenant species and host monk parakeets benefit of resultant interspecific colonianism. Part of this work have been published in the next journals: *PloS One* (2014); *Hystrix* (2014), *Royal Society Open Science* (2018).

In the **Section 2**, we recorded several adaptive strategies from several populations of three different non-native parrot species (monk parakeet, rose-ringed parakeet, and orange-winged amazon) to assess their role as facilitators of establishment and invasion processes of these parrot species against unsuitable environmental conditions. We address particular questions such as (i) whether the emergence of nesting association between monk parakeets and a native species, the white stork, depends of habitat features (rural and urban) and what benefits provide nesting association for both species, (ii) how predation pressure from native raptors determinates the success of establishment and spread of monk parakeet (Catford et al. 2009), (iii) whether the scarcity of available nesting sites is a barrier for spread of rose-ringed parakeet, (iv) how novel nesting behaviors from some individuals spread to the rest population and may assist the invasion process of rose-ringed parakeet (Lefebvre et al. 2004), (v) how an incipient non-native population of orange-winged amazon overcomes the mate shortage and other Allee effects (Courchamp et al. 1999), and (vi) whether hybridization between non-native parrot species may rescue populations in early stages of establishment (Luquet et al. 2011). Part of this work has been published in *Frontiers in Zoology* (2020).

In the **Section 3**, we infer the role of non-native parrot species in animal-plant mutualisms, in which, parrots may play a role as seed dispersers by different mechanisms. We address particular questions such as (i) which seed dispersal mechanisms are widely present between different parrot species (i.e. epizoochory and estomatochory) (Tella et al. 2015), (ii) whether parrots are promoters of secondary dispersal through food wasting when other animal species benefit of food facilitation, and (iii) how non-native parrot species may disrupt animal-plant interactions established between native biota and assist non-native plants in invasional meltdown processes (Traveset and Richardson 2014). Part of this work has been published in *Scientific Reports* (2019).

In the **Section 4**, we assess through population viability analysis the efficiency of different management actions according to a hypothetical eradication plan focused on an invasive population of rose-ringed parakeet in Seville, Spain. Given ecological impacts showed in Section 1 and ethic discrepancies regarding management actions, it is urgently necessary a consensus based in scientific-technical terms. We address particular questions such as (i) what demographic impacts show different management actions (i.e. breeding failure or removing individuals) on rose-ringed parakeet population(ii) whether population size of invader determinates the effectiveness of alternative removing individuals methods (i.e. trapping and shooting), and (iii) whether eradication plans are more feasible than control plans as well as more effective at long-term approach both conservation and cost-benefit perspectives (Simberloff 2003).

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SECTION 1:

BIOTIC INTERACTIONS IN CAVITY NESTER COMMUNITIES

Chapter I

Crowding in the city: losing and winning competitors of an invasive bird

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ABSTRACT

Invasive species can take advantage of resources unexploited by natives (opportunism hypothesis) or they can exploit the same resources but more aggressively or efficiently (competition hypothesis), thus impacting native species. However, invasive species tend to exploit anthropogenic habitats that are inefficiently used by natives such as urban environments. Focusing on the ring-necked parakeet (*Psittacula krameri*), one of the most invasive birds worldwide, we combined observations of interspecific aggressions, species-specific cavity-nest preferences and the spatial distribution of the native cavity-nesting vertebrate community to determine the invasion process as well as its potential impacts on native species in a Mediterranean city. Our results support the competition hypothesis, suggesting that ring-necked parakeets are outcompeting native species sharing nest-site preferences. Parakeets initiated and won most interspecific aggressions, which were directed towards competitors but also towards predators. This behaviour could explain the spatial arrangement of natives, with most bird species breeding close to parakeets possibly to take advantage of their effective antipredatory behaviour. However, temporal and spatial patterns of segregation suggest that a threatened bat species is negatively affected by parakeets. This demonstrates that common species gain benefits and threatened ones (in this study, a bat and possibly a falcon) lose nest sites due to invaders. Therefore, the conservation status of the native species that pay the costs of competition with invaders should be considered. This scenario of winners and losers may, however, shift towards more losers if the ring-necked parakeet population continues to grow, thus requiring close monitoring and control/eradication programs to avoid further impacts.

INTRODUCTION

Biological invasions are considered a major threat to global biodiversity, since invasive species may cause negative impacts on natives through increased predation risk, competition, hybridization or the spread of disease (Mack et al. 2000). At smaller scales, however, the relationship between invasive species and biodiversity measures is less clear (Rosenzweig 2001), as introduced species can contribute to species gain by its establishment (Sax et al. 2002), can reduce species richness through extinction processes (Claveri et al. 2009) or can have no detectable effects on native biota (Simberloff 1981). These different patterns may be explained by the nature of the invader (Sax and Gaines 2008) but also by the characteristics of the recipient community (Catford et al. 2009). In an opportunistic scenario (formally called the empty niche, the invasion window or the opportunity window hypotheses; Catford et al. 2009), invasive species are functionally different from species already present in the community and thus their entrance into a new environment can occur without the displacement or extinction of natives. Conversely, when exotic and native species exploit similar resources, the recipient community could resist an invasion as a result of competition that stems from high local diversity and low niche vacancy (MacArthur 1970; Hierro et al. 2005). However, if exotic species are able to out-compete natives by exploiting resources more efficiently or through aggressive behaviours, they can successfully invade the new area causing the displacement of the native competitor (van Wilgenburg et al. 2010).

Urban environments represent a challenge to biodiversity, as not all native species inhabiting the surrounding rural habitats are able to colonize these areas (Carrete and Tella 2011). Different studies have found a reduction in richness and diversity of native species along urban gradients, often in parallel with increments in exotic invasive ones (McKinney 2006). Thus, as cities expand across the globe, biological homogenization increases as a consequence of the widespread increment of urban-adaptable, often invasive species at the expense of native, often endemic ones (McKinney and Lockwood 1999). This pattern suggests that many exotic and native species may not compete in nature (Blackburn et al. 2009), as the former tend to be particularly abundant in habitats that are inefficiently used by natives, such as in urban environments (Sol et al. 2012). However, cities still serve as refuges and conservation areas for some endangered natives (Miller and Hobbs 2002), which might come into conflict with invasive species using highly similar resources.

Ring-necked parakeets (*Psittacula krameri*) are native to Asia and Africa and have established non-native urban populations in at least 35 countries on five continents (Butler 2003). Although it is considered amongst the 100 worst alien species in Europe (http://www.europe-aliens.org/speciesTheWorst.do), its impact on native species remains unclear. The ring-necked parakeet requires medium-size (4–8 cm entrance size, Strubbe and Matthysen 2009) natural cavities or those excavated in trees by other species for breeding. Given the usual shortage of tree cavities (Newton 1998), especially in urban environments where decaying tree limbs are periodically removed in the interests of public safety (Davis et al. 2013), parakeets could outcompete native cavity-nesting species in aggressive interactions and thus spread at the cost of the numbers and/or distribution of natives (competition hypothesis). Alternatively, if the native community is poor in secondary cavity nesters and/or the resource is not limited, the establishment of this invasive species could be facilitated by a high availability of nesting sites (opportunism hypothesis). Previous work has shown that parakeets can outcompete only one of the coexisting native cavity-nesting bird species in a central-European city (Strubbe and Matthysen 2007, 2009), but larger-scale studies comparing areas occupied and not occupied by this invader suggest little or no impact on populations of native birds (Strubbe et al. 2010; Newson et al. 2011).

The outcome of invasive-native competition could be context-dependent, being influenced by the availability of resources and the composition of the native community (Catford et al. 2009). Thus, answering similar questions but using different systems can help to make generalizations about processes from local patterns. Here, we combined observations of interspecific aggressive interactions, species-specific cavity-nest preferences and the spatial distribution of cavities available and used by each species to infer the process as well as the consequences of ring-necked parakeet invasions in a Mediterranean city. Results show a complex scenario where, although ring-necked parakeets outcompete native species in aggressive encounters, most natives seem to benefit from the effective anti-predator behaviour of parakeets. Conversely, some threatened native species can be displaced by parakeets, resulting in a dynamic process of winners and losers linked to the population growth of the invader.

MATERIAL AND METHODS

Ethics Statement

Field work conducted here was not invasive and did not require the manipulation of live animals. Therefore, this work did not require specific permits by the relevant Spanish authorities.

Study System

The ring-necked parakeet was a commonly traded wild species for the Spanish cage-bird market (Carrete and Tella 2008a) and a number of urban populations arose largely from accidental escapes from cages (Martí and del Moral 2003). This study focuses on the city of Seville (southern Spain), where the first records of the species date back to the early 1990’s and the initially small population sharply increased (Authors’ unpublished data), reaching ca. 1,000 individuals in 2011 (P. Edelaar com. pers.). We conducted the first breeding census of the species in the city of Seville from March to July 2013. We first located potential breeding areas where the species was present taking advantage of its conspicuous behaviour. Then, we monitored the available cavities to assess whether or not they were occupied by parakeets based on the observation of adults entering a minimum of 10 times on different days, the vocalizations of chicks inside the nest, and/or the observation of juveniles at the entrance. We located 216 active nests, 159 (73.6%) in an urban park (the María Luisa Park; 37° 22′ 31.57" N, 5° 59′ 19.59" W) and the rest forming smaller breeding nuclei in scattered groups of trees or, more rarely, in buildings throughout the city. María Luisa is the largest park located in the core of the city, comprising a 40 ha wooded area with a variety of tree species, most of them exotics such as *Platanus* sp., *Eucalyptus* sp. or *Gleditsia triacanthos*. The park is completely surrounded by streets with moderate to high traffic intensity.

Availability and Occupancy of Tree Cavities

The assessment of the availability of tree cavities and their occupancy by parakeets and native species was restricted to María Luisa Park to avoid potential biases when analysing interspecific competition (e.g., small groups of trees outside of the park occupied by parakeets could not be occupied by some native species because they did not offer sufficient foraging habitat). We GPS located (±3 m) all tree cavities that we were able to visually inspect in trees located within the park by using 10×50 binoculars. In each case, we identified the tree species and estimated the height of the cavity above ground (in m) and the width of its entrance (in cm). The entrances of cavities were categorized as small, medium or large (<4 cm, 4–8 cm, and >8 cm, respectively) according to previous studies, which showed the preference of parakeets for cavities with entrances between 4 and 8 cm width (Strubbe and Matthysen 2007; Czajka et al. 2011). Cavities located at <2.5 m above ground were not considered for analyses since their accessibility to humans would preclude its use (none were occupied by native or exotic species), thus biasing results. From January to August (covering the entire breeding season of native and exotic species), we repeatedly visited and observed at a distance (for a minimum of 10 min) each cavity on at least 10 different days during daylight hours to assess whether or not it was occupied and by what species, devoting 48 days (202.5 hours) of field work. The close proximity of many trees with cavities often allowed us to monitor several trees simultaneously. A cavity was considered as occupied by a given bird species when we observed adults entering a minimum of 10 times on different days, heard chicks inside, or observed juveniles at the entrance. In addition, María Luisa Park is also inhabited by the greater noctule (*Nyctalus lasiopterus*). This cavity-breeding forest species is the largest European bat (averaging 48 g; Ibáñez et al. 2001), and the whole population living in and around Seville (roughly estimated at ca. 500 individuals in 2003–2004) gathers to breed and roost communally in the tree cavities of this park (Popa-Lisseanu et al. 2008; Ibáñez et al. 2009). To identify the cavities used by greater noctules, we detected their presence using an ultrasound detector (Pettersson D 230) and observing bats leaving tree cavities at sunset. Greater noctules, like other forest bats, form fission-fusion societies that switch roosts every few days, so each bat colony can control a large number of roosts of which only a few are occupied at a specific time (Popa-Lisseanu et al. 2008). Thus, using previous information on radio-tracked individuals (Popa-Lisseanu et al. 2008), we considered that a tree was not used by greater noctules during spring-summer 2013 if we did not observe activity during any of our 10 spaced visits. Using information on trees used by noctules during 2003–2004, we also tested for changes in their use in relation to the current nesting spatial distribution of ring-necked parakeets. These trees were located after monitoring 27 noctules through radio-tracking to study the spatial pattern of tree use by the species, finding that cavities located in 75 trees were alternatively used as roost sites ten years ago (Popa-Lisseanu et al. 2008). It is worth noting that the different methodologies used to identify occupied trees could produce false cases of inoccupation in both 2003–2004 (a larger period of time monitoring 27 individuals) and 2013 (a shorter period of time monitoring all tree cavities). However, it may also just produce statistical noise making our estimates conservative.

Spatial Distribution of Occupied Cavities

The occupancy of a particular tree cavity by a given species could be influenced by the spatial distribution of cavities occupied by the same and/or other species, driven not only by competition but also by conspecific and heterospecific attraction processes. We thus obtained the distance from each occupied cavity to the nearest cavity occupied by conspecifics and heterospecifics (nearest neighbour distance) as well as the corresponding nest aggregation indexes. These aggregation indexes were obtained as the relative position of each occupied cavity within the whole distribution of all cavities occupied by conspecifics or heterospecifics in the park using $\sum exp\ (-dij)$, with $(i \neq j)$ where dij is the linear distance between occupied cavities i and j, j representing all occupied cavities (Moilanen and Hanski 1998). These variables were complementary measures depicting the social environment around each nest cavity at a landscape scale as well as the existence of close competitors.

The spatial distribution of occupied cavities could also be influenced by habitat heterogeneity in the park. We considered the two main sources of habitat heterogeneity in our study area, i.e. the proximity to surrounding streets and forest cover. Noise from car traffic could alter song performance, reproductive success and even the spatial distribution of birds (Slabbekoorn and Peet 2003; Halfwerk et al. 2011). We therefore measured the linear distance from each cavity to the closest street using GIS tools (see below). On the other hand, species could differ in their preferences for forest coverage around cavities. We obtained forest cover by measuring it in a radius of 30 m around each GPS located cavity on a Google Map image taken in 2013 (Imagens ©2013 Cnes/Spot Image, DigitalGlobe, Instituto de Cartografía de Andalucía, map data ©2013 Google, based on BCN IGN Spain), using OpenLayers Plugin (1.1.0) applications in Q-GIS 1.8.0 (2008 Free Software Foundation, Inc). Forest cover was then scored into four main categories, namely 0–25%, 25–50%, 50–75%, and 75–100%.

Interspecific Interactions

We assessed interspecific interactions by randomly sampling the behaviour of different nesting ring-necked parakeets during a 15-minute period. We conservatively recorded the bird species present within a radius of 15 m around the focal parakeet, whether or not there was an aggressive interaction, what species started the attack, and which was the winner. To increase sample size without resampling the same individuals or the number of potential interacting species, observations were conducted in María Luisa Park as well as in other urban areas of Seville occupied by the species (see above), totaling 88 days (351.5 hours) of field work. These areas included the main parks of the city as well as a church (Divino Salvador) where ring-necked parakeets occupied cavities in walls for breeding, potentially competing there with lesser kestrels (*Falco naumanni*), a colonial falcon that usually breeds in urban buildings (Tella et al. 1996).

Statistical Analysis

We employed Generalized Linear Models (GLM) implemented through the GENMOD procedure in SAS 9.2 (SAS Institute 2008) to ascertain which variables determined hole occupation, using the binomial error distribution (cavity occupied or not occupied by a given species) and the logistic link function. In a first set of models, we aimed to determine whether occupied and vacant cavities differed in their structural characteristics. Thus, we modelled the probability of occupancy as a function of the height of the cavity above ground (in its linear and quadratic forms), the entrance size, and the tree species. The resulting species-specific patterns of cavity preferences (see results) made it difficult to identify similarities (and thus opportunities for competition) between species. Therefore, we performed a categorical principal component analysis (CATPCA) on entrance size (since it is a categorical variable) and height above ground of the cavities occupied and took the scores of the obtained first dimension as a single compiling descriptor of the cavities used by each species. An ANOVA on these scores allowed us to identify differences in cavity preferences among species, and post-hoc Scheffe tests permitted us to establish homogeneous groups (i.e., species not differing in their preferences for particular cavity traits). In a second set of models, we assessed the spatial arrangement of each species regarding cavity traits, the distribution of both conspecifics and heterospecifics, and main habitat features (distance to the nearest street and forest cover) around each occupied and available (i.e., unoccupied) cavity, also using GLMs with a binomial error distribution and logistic link function.

Exact binomial tests were used to assess whether the proportion of interspecific encounters ending in aggressions, the proportion of aggressions initiated by ring-necked parakeets, and the proportion of aggressions won by this species differed significantly from parity. To obtain interspecific patterns in the frequency of aggressions and their outputs, we also used GLMs with a binomial error distribution and a logistic link function, fitting as explanatory variables the average body mass of the species interacting with ring-necked parakeets (obtained from Dunning 1993), their overlap in nest-site preferences (as a factor with levels ranging from 0– the interacting species was not a cavity-nester- to 3– maximum overlap in nest-site traits), and whether the interacting species was a potential predator of eggs, nestlings or adults. We expected that ring-necked parakeets would be more prone to attack those species with overlapping nest-site preferences and potential predators, and less prone to attack larger-bodied species.

A backward procedure was performed for GLM modelling, removing from full models those variables that were non-significantly associated with the response variable ($p>0.05$) to obtain minimum adequate models (MAM) (Sol et al. 2012). The resulting models did not show data overdispersion. We calculated the percentage of deviance explained as a measure of the variance explained by each MAM.

RESULTS

Occupancy of Tree Cavities

We recorded 1,086 cavities in 435 trees located within María Luisa Park during the 2013 breeding season. Cavities were located at an average height above ground of 13.09 (SD 5.51) m, and the commonest cavity entrances (47%) were of intermediate size (4–8 cm). Most cavities (62.2%) were located in London plane trees (*Platanus* × *acerifolia*) probably because it is the most abundant species within the park but is also the species with highest number of available cavities.

A total of 10 species were found occupying 525 cavities (Table 1), including 9 bird and one bat species. Two bird species were exotics, i.e. the ring-necked parakeet and the blue-crowned parakeet (*Aratinga acuticaudata*). Ring-necked parakeets, feral pigeons (*Columba livia* var. *domestica*), house sparrows (*Passer domesticus*), and greater noctules showed the largest percentages of occupied cavities, while the rest of the species used less than 10% of occupied cavities (Table 1).

Table 1. Number and percentage of cavities occupied by each species during the 2013 breeding season in María Luisa Park (Seville, Spain).

Species	N of occupied cavities	%
BIRDS		
Ring-necked parakeet (*Psittacula krameri*)	159	30.29
Blue-crowned parakeet (*Aratinga acuticaudata*)	2	0.38
Tawny owl (*Strix aluco*)	1	0.19
Feral pigeon (*Columba livia* var. *dom.*)	133	25.33
Geat tit (*Parus major*)	13	2.48
Blue tit (*Cyanistes caeruleus*)	9	1.71
Short-toed treecreeper (*Certhia brachydactyla*)	2	0.38
House Sparrow (*Passer domesticus*)	105	20
Spotless starling (*Sturnus unicolor*)	45	8.57
BATS		
Greater noctule (*Nyctalus lasiopterus*)	56	10.67
TOTAL	525	

Species Partitioning of Tree Cavities

More than half of the cavities (51.7%, n=1,086) were unoccupied during the study period. However, occupied cavities significantly differed from unoccupied ones in terms of entrance size and height above ground, both considering all species together and each species from which the sample size allowed us to build separate GLMs (Table 2). Figure 1 illustrates the direction of the effects. Except for house sparrows, most species seemed to prefer cavities located at greater heights than those available (i.e., unoccupied by any species). Entrance size of occupied and available cavities also varied among species. Great (*Parus major*) and blue tits (*Cyanistes caeruleus*) only used small-size cavities, feral pigeons made more use than expected of the large ones, while ring-necked parakeets, spotless starlings (*Sturnus unicolor*) and greater noctules seemed to prefer medium-sized cavities. Although traits of occupied and available cavities also differed significantly in the case of house sparrows (Table 2), this species was distributed more evenly, nesting in cavities of different sizes (Figure 1). Tree species and the interactions among variables did not predict cavity occupancy by any species, since these terms were not retained in the MAM (Table 2).

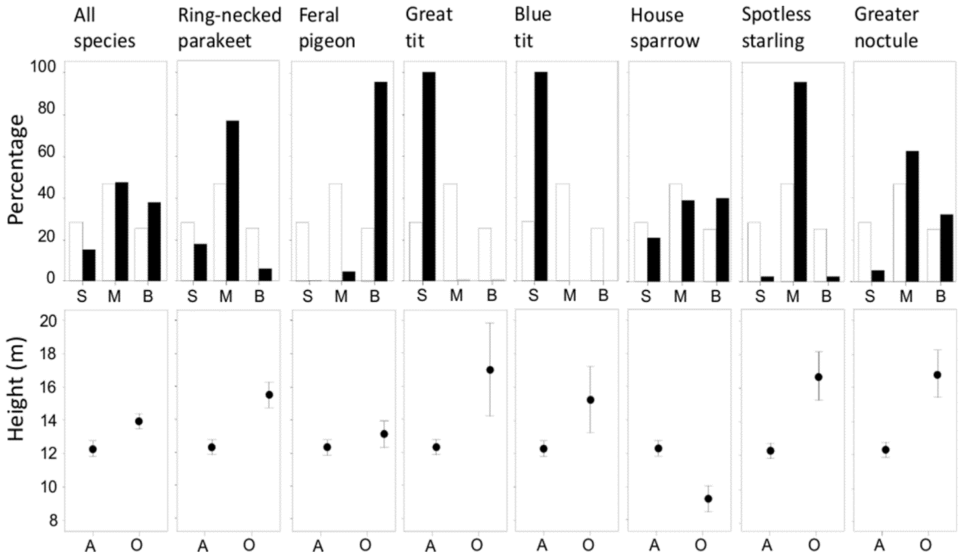

Figure 1. Differences in cavity size (small, medium, and big) and height above ground (mean and 95% CI) between tree holes occupied (black bars) and available (white bars) during the 2013 breeding season. All figures are depicted at the same scale to allow easier inter-specific comparisons.

Table 2. GLMs obtained to explain the probability of cavity occupancy by a given species and by all species together as a function of cavity traits (entrance size and height) and tree species.

	Size		**Height**		**%dev**
	χ^2 (df = 2)	**P**	**χ^2 (df = 1)**	**P**	
All species	37.38	<0.001	26.07	<0.001	4.08
Ring-necked parakeet	40.97	<0.001	25.5	<0.001	10.52
Feral pigeon	256.6	<0.001	9.11	0.0025	38.19
Great tit	32.85	<0.001	8.31	0.0039	32.62
Blue tit	22.45	<0.001			24.26
House sparrow	6.65	0.036	30.21	<0.001	6.82
Spotless starling	40.6	<0.001	15.23	<0.001	19.86
Greater noctule	16.65	0.0002	27.79	<0.001	12.18

The number of cavities occupied by each species is reported in Table 1, and the number of unoccupied (available) cavities was 561. % dev: percentage of deviance explained.

The first dimension obtained in a CATPCA (eigenvalue=1.12) explained 56.1% of variance of the combined traits of occupied cavities, positively correlating with entrance size (r=0.99) and negatively with height above ground (r=−0.21). Using the scores of this dimension as a single descriptor of cavity traits, we found significant differences among cavities occupied by the different species (ANOVA $F_{6,513}=69.99$, $P<0.001$). A post-hoc Scheffe test identified three homogenous subgroups where the species belonging to each one did not differ in the characteristics of the cavities used: 1) ring-necked parakeet, spotless starling and greater noctule (P=0.92), 2) great and blue tits (P=0.99), and 3) feral pigeon and house sparrow (P=0.93).

Spatial Arrangement of Species

The above results suggest evidence for competition for certain kinds of cavities within the three subgroups of species considered. However, the actual occupancy of cavities by each species may also be influenced by the spatial distribution of conspecifics and heterospecifics, through social interactions that may range from agonistic encounters to hetero- and conspecific attraction, and by habitat features around cavities. Models considering the distance to the nearest occupied cavity (D) and the surrounding aggregation of occupied cavities (A) by conspecifics or heterospecifics, while controlling for habitat features (Table 3), were better to explain the probability of cavity occupancy (see % of deviance explained) than those just relying on cavity traits (Table 2). While habitat features were only related to the spatial distribution of three species (great tit, house sparrow, and spotless starling), all species seemed to be influenced by the spatial distribution of other birds, and in two species (blue tit and house sparrow) some cavity traits even dropped from models when the social environment was taken into account (Table 3). The probability of cavity occupancy decreased at greater distances from conspecifics (D_{intra}) in all species except the blue tit, which tended to avoid large conspecific aggregations (A_{intra}).

Table 3. GLMs explaining the occupancy of cavities by each species as a function of cavity traits, cover of forest canopy, distance to the nearest street, distance to the nearest occupied cavity (D), and aggregation of occupied cavities around the focal one (A).

	Cavity size	Cavity height	Forest cover	Distance street	Dintra	Aintra	Dinter	Ainter	% dev
Ring-necked parakeet	35.58***	4.75*			144.01 (-)***			7.89 (-)***	29.47
Feral pigeon	243.54***	18.27***			7.36 (-)***	65.79 (-)***	27.92 (-)***	42.81 (+)***	51.04
Great tit	15.85***	12.93***		5.27 (-)*	6.01 (-)*	35.31 (-)***		15.35 (+)***	68.11
Blue tit	16.87***					49.99 (-)***		27.25(+)***	78.59
House sparrow		21.08***	13.51***	10.97 (+)***	31.04 (-)***		15.71 (-)***	21.04 (-)***	31.74
Spotless starling	37.41***	18.01***		15.14 (+)***	4.58 (-)*	62.82 (-)***	12.41 (-)***	4.48 (+)*	48.45
Greater noctule	17.02***	18.55***			40.14 (-)***		5.69 (+)**		22.91

Variables describing social environments (A and D) were obtained considering cavities occupied by the same species (intraspecific; A_{intra}, D_{intra}) and by the ring-necked parakeet (A_{inter}, D_{inter}). The species involved in interspecific significant effects (A_{inter}, D_{inter}) was always the ring-necked parakeet, except in the case of the model obtained for this species, where A_{inter} corresponds to the aggregation regarding greater noctules. Signs between brackets indicate positive or negative effects of variables on the probability of cavity occupancy. χ^2 values are given for each variable; *: $p<0.05$, **: $p<0.01$, ***$p<0.001$; % dev: percentage of deviance explained.

Interspecific effects on spatial distributions differed among species (Table 3). For most bird species, the probability of cavity occupancy increased at closer distances to the nearest cavity occupied by ring-necked parakeets and/or the larger the aggregation of the invader (except for house sparrows, which seemed to avoid large aggregations of ring-necked parakeets). However, cavity occupancy by greater noctules was higher the greater the distance to cavities occupied by ring-necked parakeets, and cavity occupancy by ring-necked parakeets was lower the greater the spatial aggregation of greater noctules, thus suggesting a process of spatial segregation between these two species.

Temporal Changes in the Spatial Distribution of Greater Noctules

As the available data for the period 2003–2004 was restricted to trees holding cavities occupied by greater noctules, our analyses of changes in occupancy were done at the tree scale. From 75 trees occupied 10 years ago, 49 were unoccupied by noctules in 2013 despite they still offered suitable cavities, which implies a loss of ca. 39% of occupied trees during the last 10 years. The probability that a tree was abandoned during this period was higher the greater the distance to the nearest tree occupied by noctules (estimate=−79.93, SE=33.13, χ^2=5.82, P=0.016) and the smaller the aggregation of trees occupied by noctules in 2013 (estimate=0.23, SE=0.11, χ^2=4.07, P=0.044). Interestingly, the probability of tree abandonment was also positively related to the presence of ring-necked parakeets nesting in the same tree in 2013 (estimate=2.35, SE=0.85, χ^2=7.58, P=0.006), and to the aggregation of trees occupied by parakeets around the tree previously occupied by noctules (estimate=−0.15, SE=0.07, χ^2=5.34, P=0.021) (deviance explained=24.30%). Indeed, 20 trees abandoned in 2013 by noctules were occupied by ring-necked parakeets, while only 2 of the trees that remained occupied by bats were also shared with the invasive species.

Interspecific Aggressions

We recorded 435 encounters between nesting ring-necked parakeets and 13 bird species that approached within ≤15 m (Table 4). Three of them (blue-crowned parakeet, monk parakeet and Senegal parrot) were also exotic parrots. Four species were potential predators of adult birds or their eggs and nestlings (booted eagle, black kite, lesser kestrel and jackdaw), the last two also breeding in cavities (Table 4).

Table 4. Bird species that encountered nesting ring-necked parakeets during the 2013 breeding season in urban areas of Seville.

	Body mass	Predator	Cavity nester	Nesting overlap	# encounters
Ring-necked parakeet (*Psittacula krameri*)	116.5				
Spotless starling (*Sturnus unicolor*)	80	No	Yes	3	91
Feral pigeon (*Columba livia* var. *dom.*)	354.5	No	Yes	1	80
Lesser krestel (*Falco naumanni*)	152.5	Yes	Yes	2	73
House sparrow (*Passer domesticus*)	27.7	No	Yes	2	66
Jackdaw (*Corvus monedula*)	246	Yes	Yes	2	38
Senegal parrot (*Poicephalus senegalus*)	147	No	Yes	3	33
Eurasian collared dove (*Streptopelia decaocto*)	149	No	No	0	16
Blue-crowned parakeet (*Aratinga acuticaudata*)	165	No	Yes	3	10
Blue tit (*Cyanistes caeruleus*)	13.3	No	Yes	1	8
Black Kite (*Milvus migrans*)	827	Yes	No	0	7
Monk parakeet (*Myiopsitta monachus*)	101	No	No	0	7
Great tit (*Parus major*)	19	No	Yes	1	4
Booted eagle (*Aquila pennata*)	834.5	Yes	No	0	2

The average body mass of the species (in g), whether or not they can predate ring-necked parakeets (eggs, chick or adults) and are cavity nesters, as well as their overlap of nesting preferences and numbers of encounters are reported.

Almost half (42.5%, n=435) of the encounters ended in aggressive interactions. Most aggressions were initiated by ring-necked parakeets (69.2%, n=185; binomial test P<0.001), and this species won most of the fights (83.8%, n=185, binomial test P<0.0001). However, the output of these encounters greatly varied among the interacting species (Figure 2). When considering the traits of the interacting species and the number of ring-necked parakeets and of the interacting species involved in encounters (Table 5), the probability that an encounter ended in aggression increased with the interspecific overlap in nest type preferences and the body mass of the interacting species, and decreased with the number of individuals of the interacting species involved. The probability that an aggression was initiated by ring-necked parakeets decreased with the body mass of the interacting species. Finally, the probability that a fight was won by ring-necked parakeets was greater if they initiated the attack but decreased when the interacting species was a potential avian predator. Nonetheless, ring-necked parakeets won 25–100% of the aggressions directed towards different predator species (Figure 2).

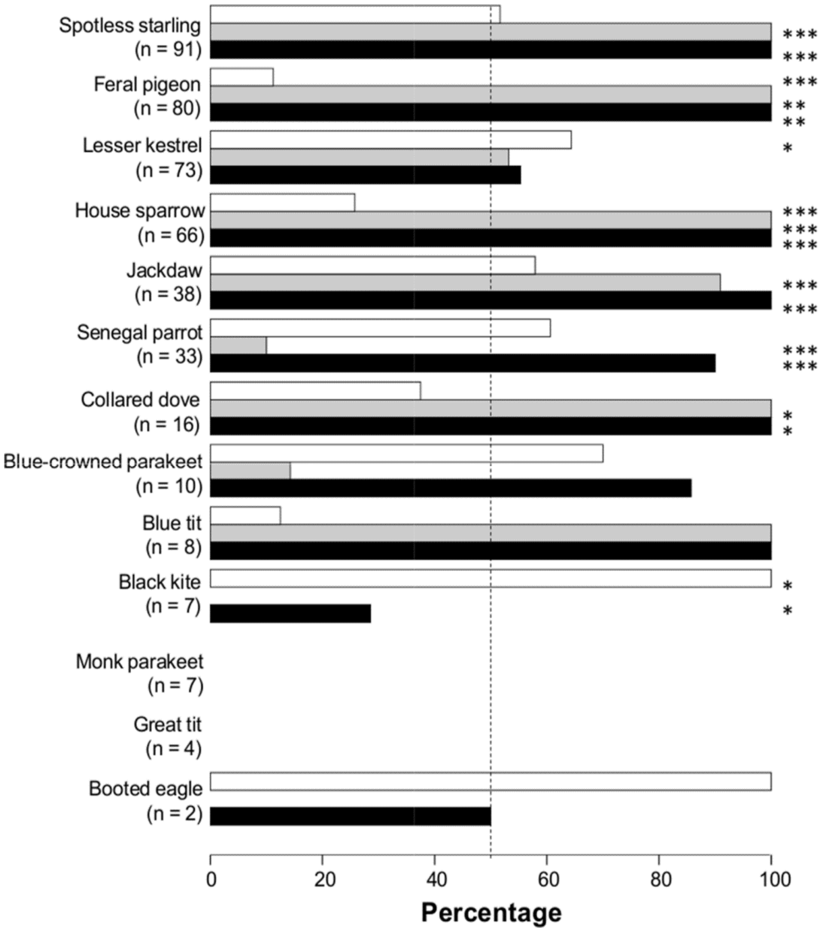

Figure 2. Percentage of encounters with ring-necked parakeets that ended in aggressions (white bars), and percentage of aggressions initiated (grey bars) and won by ring-necked parakeets (black bars). The number of recorded encounters is shown in brackets.

Table 5. GLMs explaining the probability that an interspecific encounter ended in aggression (Aggression), whether the aggression was initiated by ring-necked parakeets (Fight initiation) and was won by ring-necked parakeets (Win fight).

	Nesting overlap	**N**	**Body mass**	**Attack initiation**	**Predator**	**% deviance**
Aggression	78.83 (+)***	17.13 (-)***	27.24 (-)***			19.32
Fight initiation			21.89 (-)***			9.58
Win fight				24.7 (+)***	27.89 (-)***	37.02

The retained explanatory variables were the interspecific overlap in nest types (Nesting overlap), the number of individuals of the interacting species present in the encounters (N), the average body mass of the interacting species (Body mass), whether or not ring-necked parakeets initiated the aggression (Attack initiation), and whether or not the interacting species is a potential predator of birds. χ^2 values are given for each variable. Signs between brackets indicate positive or negative effects of the explanatory variables. ***: p<0.001; % dev: percentage of deviance explained.

DISCUSSION

Opportunism or Competition?

The successful establishment of exotic species in novel habitats constitutes a poorly understood paradox (Sax and Brown 2000). Recently, Sol et al. (2012) examined the invasion paradox by studying the use of food resources by invasive and native bird species in an Australian city, concluding that the success of invaders is explained by their capacity to exploit ecological opportunities that most native species rarely use. However, as the authors pointed out, competition over other resources, notably nesting sites, must be considered in further studies (Sol et al. 2012).

We investigated two key aspects behind the establishment success of ring-necked parakeets on a relatively newly invaded urban area, namely: the way they shared nest-site resources with the recipient community and the aggressive interactions they experienced with other species. This approach allowed us to show that this species may invade new areas even when resources are not overabundant, thus not supporting the hypotheses proposing that saturated communities can halt biological invasions through competitive processes but rather supporting the competition hypothesis (instead of the opportunism hypothesis) for successful invasions (Catford et al. 2009). Although the availability of tree cavities was relatively high in the study area compared to other cities (Strubbe and Matthysen 2009; Orchan et al. 2013), the large populations sizes of different cavity-nester species together with the fact that the characteristics of unoccupied cavities differed from those of occupied ones suggest a shortage of suitable breeding sites for the native cavity-nesting community, coincident with the general pattern of competition found across cavity-nesting communities especially in urban environments (Newton 1994; Strubbe and Matthysen 2009; Orchan et al. 2013). Most of the inability of the native community to resist the parakeet invasion may be due to the invader's highly aggressive behaviour that allows it to out-compete natives, thus successfully occupying areas even when there is no superabundant or underexploited resources. Interestingly, we were able to separate species into three main functional groups based on species-specific nest site requirements, showing that parakeets fit into one of these groups. Thus, even when they may be interacting with many native species, they share important resources for population prospects (i.e., reproduction) with only some of them. However, ring-necked parakeets were aggressive (and won most aggressive encounters) not only towards those species sharing nest-site preferences (including two other exotic parrot species) but also towards others, even non cavity-nesting species and avian predators. Therefore, the ring-necked parakeet has the potential to modify the numbers and spatial distribution of coexisting breeding species through behaviour-mediated competitive exclusion.

Mechanisms behind the Spatial Arrangement of Species

Habitat selection models, and species distribution models in their broader sense, are mathematical descriptions of biological patterns that are affected by environmental conditions and a multitude of direct and indirect interactions (Diamond 1975), thus inferring that causal links from observational data should be made with caution. Two species may co-occur if they share their habitat requirements, but also if they facilitate each other directly or indirectly. Conversely, species may appear to avoid each other if they show competitive exclusion but also if they have dissimilar habitat requirements. Although competition for cavities can trigger intraspecific negative interactions among individuals, we detected a general tendency among species to breed following a pattern of conspecific aggregation. This seems not to result from heterogeneities in habitat and nest site availability, aspects which were controlled for in statistical analyses, and thus may rather be related to conspecific attraction processes as previously observed in many other colonial but also territorial species (e.g. Stamps 1988; Serrano et al. 2004). Different studies have shown that breeding in close proximity to conspecifics benefits breeders from earlier detection of predators, group defence, and dilution of predation (Brown and Brown 2001; Krause and Ruxton 2002; Serrano et al. 2005).

Regarding the effects of the invasive species, we found that the spatial distribution of nesting ring-necked parakeets was important to explain the distribution patterns of all tree-cavity nester species of the recipient community while controlling for the main habitat features. However, the underlying putative mechanisms (attraction or segregation) were different among species. All bird species increased their likelihood of occupying cavities located close to parakeet nests and/or to high densities of parakeets. Positive co-occurrence patterns are indicative of heterospecific attraction (Sebastián-González et al. 2010), thus signaling the presence of direct or indirect species interactions. In our study system, a possible explanation for this association pattern could be found in the high aggressiveness of parakeets against avian predators. In fact, ring-necked parakeets may even communally attack predators, as we observed a flock of 60 parakeets mobbing a booted eagle (*Aquila pennata*) in María Luisa Park in 2008. Therefore, native species may choose breeding sites far enough from ring-necked parakeets (>15 m) to avoid aggressions but close enough to be rewarded by their effective anti-predator response, resulting in an active breeding association, which benefits the associated species (Blanco and Tella 1997). Conversely, the mutual spatial segregation between parakeets and noctules, not explained by habitat features, could be indicative of direct competition since they share their preferences for the same kind of cavities. The nocturnal behaviour of bats precluded the systematic observation of encounters with ring-necked parakeets, which would have been restricted to instances when parakeets would enter bat cavities and inspect for potential nest sites. Although greater noctules aerially hunt small passerines when migrating at night (Ibáñez et al. 2001), they are not able to kill birds inside their nests (J. Juste com. pers.) and even less so a much larger species such as the ring-necked parakeet whose body mass (116 g) is more than twice that of the noctule (50 g). Given that parakeets won most aggressions when encountering larger-bodied competitors such as feral pigeons and even powerful jackdaws (Figure 2), they would be expected to also win most aggressive interactions with this much smaller bat species. Although little is known about the effects of aggressive species like parakeets on mammals that shelter and reproduce in hollows like bats, several authors suggested that they can evict them (Gebhardt 1996; Start 1998) and there is concern that ring-necked parakeets could cause the loss of suitable cavities for the noctule bat (*Nyctalus noctula*) in The Netherlands (Haarsma and van der Graaf 2009). In our study area, a greater noctule was fortuitously observed being aggressively expulsed from its cavity by a ring-necked parakeet in María Luisa Park in 2005 (E. Revilla com. pers.), and it could be expected that the strong beak of parakeets could seriously injure noctules to the point of killing or impeding their flight by irreversibly damaging their sensible patagium (J. Juste com pers.). Moreover, there is a published observation of a similar body-sized exotic parakeet (Superb Parrot, *Polytelis swainsonii*) killing the much larger red squirrel (*Sciurus vulgaris*, 295 g; Palomo et al. 2007) in Italy (Mori et al. 2013) and evidence of similar cases that might had been caused by ring-necked parakeets in France (Japiot 2005; Clergeau and Vergnes 2009). During this study we observed 11 instances of ring-necked parakeets (involving up to 10 individuals) attacking and mobbing black rats (*Rattus rattus* 180 g; Palomo et al. 2007), forcing them from the proximity of their nests. Since both rats and squirrels are predators of bird nests, including those of parakeets (Mori et al. 2013), these observations also reinforce the potential benefits to other bird species of breeding close to parakeets.

Impact: Winners and Losers in a Contemporary Invasion Process

It is difficult to fully ascertain the ecological impacts of invaders, given the variety of potential impacts to be assessed, their subtle but pervasive effects, and the long time gaps between the introduction of an exotic species and its achievement of invasiveness and detectable impacts (Strayer et al. 2006; Simberloff et al. 2013). Although there are well-recognized cases of negative impacts of bird invasions in island environments (Lever 2005; Freed and Cann 2009), their impact on mainland environments have been less studied and much debated (Kumschick and Nentwig 2010; Bauer and Woog 2011; Strubbe et al. 2011), to the point of suggesting that introduced bird species should be managed before their negative impacts are proven (Edelaar and Tella 2012).

Although ring-necked parakeets have been shown to outcompete a small cavity-nesting native bird species in Brussels (Strubbe and Matthysen 2009), there is little evidence of its impact on native communities when comparing areas occupied or unoccupied by this invader (Strubbe et al. 2010; Newson et al. 2011). Our different approach, by recording the output of inter-specific aggressions and the spatial distribution of species in a Mediterranean city, suggests, however, that ring-necked parakeets may trigger strong effects on the native recipient communities, with both positive and negative responses depending on the native species considered.

The spatial segregation of greater noctules and ring-necked parakeets together with the spatial patterns of trees abandoned during the last decade by noctules, its apparent population decrease and the parallel increase in the ring-necked parakeet population (Authors unpubl. data) suggest an active displacement exerted by the invasive species. This is a matter of concern for this bat species, which shows a scattered distribution throughout Europe and is classified as Vulnerable in Spain, with María Luisa Park supporting its largest known colony (Ibáñez et al. 2004). Previous radio-tracking studies showed that greater noctules forage over large extensions of natural habitats (up to 40 km from the urban park (Popa-Lisseanu et al. 2009), including Doñana National Park and surrounding marshlands, but they return daily for roosting to Maria Luisa Park and no alternative refuges are known for this population (Popa-Lisseanu et al. 2008; 2009). This large population of greater noctules is therefore highly sensitive to any reduction in the availability of tree cavities caused by ring-necked parakeets. Given the scarcity of mature forests with large numbers of adequate cavities for the species, the other –although smaller- colony of greater noctules known in South Spain is also located in an urban park (in Jerez de la Frontera, 77 km far from Seville) (Ibáñez et al. 2001). Although the presence of ring-necked parakeets is still anecdotic in this city, its population expansion might also pose threats to this bat population in the near future. Further studies are needed to deep on the population ecology and trends of greater noctule populations, and of other bat species (Haarsma and van der Graaf 2009), related to their coexistence with invasive parakeets.

Another cause of concern is the fact that parakeets began to use wall cavities in 2011, breeding in three buildings in 2013, one of them located in the core of the city where there is also a colony of lesser kestrels. This colonial falcon suffered a drastic decline in Europe due to land-use changes that did not revert until recent years thanks to widespread conservation actions, including the provisioning of nest cavities (Catry et al. 2013). Lesser kestrels breeding in Seville have to forage far from their breeding colony (Tella et al. 1998) but gain benefits by the reduced predation risk in the city (Tella et al. 1996). Although their breeding success was linked to the quality of wall cavities (Negro and Hiraldo 1993), the species was not constrained by nest-site availability or competition with feral pigeons and jackdaws in recent decades (Forero et al. 1996). However, the newly established ring-necked parakeet fought more than expected with lesser kestrels and won more than half of the aggressive encounters (Figure 2), while occupying only six wall cavities within the lesser kestrel colony. If the parakeet population continues to grow exponentially, it may pose a serious problem for urban lesser kestrels as well. In contrast to noctules and lesser kestrels, which are forced to forage far from the city, the abundance of food resources for ring-necked parakeets in the urban parks could reduce the energy they expend, allowing an increase in their breeding success and population growth (Strubbe and Matthysen 2011), thus reinforcing their competitive superiority.

Both winner and loser species may result from anthropogenic-driven expansions of species (Carrete et al. 2010), some invaders even favoring whole communities of natives (Tablado et al. 2010). Our results suggest that the presence of nesting ring-necked parakeets may benefit several non-threatened native bird species, which may incur breeding advantages by exploiting their effective anti-predatory behavior. However, this situation could change in the near future if the ring-necked parakeet population continues to grow. This is already the most abundant species breeding in the park and is the only one able to enlarge tree cavities up to reaching its preferred size (4–8 cm; Strubbe and Matthysen 2009; Czajka et al. 2011; this study), as has been shown in other urban parks (Orchan et al. 2013). In fact, 7 out of the 28 small-sized cavities (entrance <4 cm) were enlarged and occupied by parakeets during this study. Therefore, nest sites may become limited even for species using small-sized cavities such as tits and house sparrows. The latter species is a widespread commensal whose European populations are now decreasing, thus drawing attention to its long-term conservation status (Robinson et al. 2005; Shaw et al. 2008).

Conservation Implications

We have shown potentially serious impacts of an invasive bird targeting species that are not easily monitored or that are not expected to interact with them, such as a forest bat and a colonial falcon nesting in buildings, thus highlighting the difficulties in assessing the entire set of impacts posed by invaders (Simberloff et al. 2013). The potential impact of ring-necked parakeets (Strubbe and Matthysen 2009), as well as of other parakeet species (Davis et al. 2013) thriving in urban habitats, has been often discounted since urban bird communities are usually composed by few, generalist and non-threatened species (McKinney and Lockwood 1999; Sol et al. 2012). However, our case study suggests that urban ring-necked parakeets may be negatively affecting two threatened species, with some common species probably also affected in the near future if the parakeet population continues to grow. Therefore, both the conservation status of the native species with which the invader interacts as well as the population trends of the invader should be considered. Moreover, the positive population trends of ring-necked parakeets in Spain (authors' unpubl. data) suggests, as for monk parakeets (Muñoz and Real 2006), that the species could spread and invade rural habitats, as is already the case in central Spain (authors' unpubl. data). In such cases, parakeets would interact with a wider community of non-urban species and new impacts could arise, thus requiring a close monitoring of inter-specific interactions.

As recommended for other invasive organisms (Simberloff et al. 2013), management of avian invasions should be undertaken before populations spread and actions become costly and even unaffordable (Edelaar and Tella 2012). In this regard, our results provide evidence for the need of implementing control or even eradication plans for ring-necked parakeets in Spain. A very recent law (Real Decreto 630/2013) includes this species in the Spanish Catalogue of Invasive Species and provides legal coverage for such actions. We recognize that the success of these management actions is highly dependent on social perception, and projects involving eradicating birds are usually those least supported by citizens (Bremner and Park 2007). This is exacerbated in the case of the highly charismatic urban parrots (Carrete and Tella 2008b). Therefore, efforts should be made to raise public awareness of the problem (Blackburn et al. 2010), using for this purpose not only the ecological effects but also its potential economic and health impacts (Fletcher and Askew 2007; Tayleur 2010).

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Chapter II

Alien rose-ringed parakeets (*Psittacula krameri*) attack black rats (*Rattus rattus*) sometimes resulting in death

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ABSTRACT

The rose-ring parakeet (*Psittacula krameri*) is one of the most successful invasive birds in its establishment worldwide. Studies addressing its potential impact on native biota mostly focus on birds and little is known about how these and other parakeet species interact with native mammals. Here, we report 21 aggressions of rose-ringed parakeets towards black rats (*Rattus rattus*) in urban parks in Seville (Southern Spain) and Tenerife (Canary Islands). Either solitary parakeets or, more often, groups of up to 18 attacked rats when they climbed trees close to parakeet nests. Most attacks ended when the rats descended to the ground. However, in two instances (9.5% of the aggressions) the attacks resulted in the death of the rats as a result of falling to the pavement. These observations add further complexity to a biological invasion, where introduced parakeets have negative impacts on a predator and thus, some native bird species may benefit from their antipredator behavior. More attention should be paid to the interactions between native mammals and the non-native parakeets introduced worldwide.

MAIN TEXT

Biological invasions are considered among the main causes of biodiversity loss (Clavero and García-Berthou, 2005). Since the mid twentieth century, the introduction of exotic species has accelerated at an alarming rate (Hulme, 2009), mainly as a consequence of international trade (Meyerson and Mooney, 2007). Wild birds are among the most commonly traded vertebrate taxa (Carrete and Tella, 2008a), with a number of species having been accidentally introduced in recent times (Carrete and Tella, 2008b; Blackburn et al., 2010). Among these, parrots are one of the most heavily traded groups, mainly because of their attractiveness as pets (Tella and Hiraldo, 2014). Thirty-eight percent of birds offered for sale in Spanish pet shops between 2004 and 2005 were parrots belonging to 72 different species (Carrete and Tella, 2008b). Not surprisingly, several parrot species have established non-native populations worldwide (Lever, 2005; Menchetti and Mori, 2014).

Introduced parrots may have a variety of ecological and economic impacts (Menchetti and Mori, 2014). Regarding ecological impacts, most research focuses on how introduced parrots affect native avifauna (e.g., Strubbe and Matthysen, 2007, 2009; Hernández-Brito et al., 2014). However, very little information is available on how they interact with native mammals. Mori et al. (2013) observed red squirrels preying on chicks at two rose-ringed parakeet (*Psittacula krameri*) nests, while an adult Barraband's parakeet (*Polytelis swainsonii*) was responsible for the death of an adult red squirrel (*Sciurus vulgaris*) in Italy. Another report documents rose-ringed parakeets killing an adult red squirrel in France (Clergeau et al., 2009). More recently, Menchetti et al. (2014) recorded a fatal attack by a rose-ringed para keet of a Leisler's bat (*Nyctalus leisleri*) in Italy. Here, we report several cases of rose-ringed parakeets attacking and even causing the death of black rats (*Rattus rattus*) in Spain.

Observations of aggressions by non-native rose-ringed parakeets towards black rats were made in 2011, 2012, 2013 and 2014 in urban parks of Seville (Southern Spain), and Santa Cruz de Tenerife (Canary Islands). The two parks in Seville in which aggressions were recorded were Royal Alcázar (37°23'1.8"N / 5°59'29.6"W) and María Luisa Park (37°22'31.57"N / 5°59'19.59"W). Rose-ringed parakeets breed in both parks, with María Luisa Park holding the largest breeding nucleus in Seville (159 active nests in 2013; Hernández-Brito et al., 2014). Observations in Santa Cruz de Tenerife were made at García Sanabria Park (28°28'19"N / 16°15'13"W), where the breeding population of rose-ringed parakeets reached 12 pairs in 2014 (D. Hernández-Brito, unpubl. data).

We observed 21 aggressions and attacks of rose-ringed parakeets on black rats, 16 in Seville and 5 in Tenerife. Interactions occurred when rats climbed trees where rose-ringed parakeets were nesting or trees in the vicinity of nests. When a rat was detected (Fig.1), rose-ringed parakeets first emitted loud alarm calls and then chased and attacked the rat using physical aggressions, sometimes biting it and producing visible wounds. All observed attacks were of solitary rats. Attacks were carried out by solitary parakeets or, more frequently, by groups of up to 18 individuals recruited from the surrounding breeding pairs (Fig.2A). In most cases, parakeets stopped the attack when rats escaped and descended or fell to the ground. Attacks caused the death of two rats in María Luisa Park. In the first event, a rat fell to the ground from a height of 15 meters when it was attacked by five rose-ringed parakeets in the treetops of a London plane. The rat fell directly onto the pavement, dying upon impact. The second rat died under similar circumstances; the rat was on a London plane with a rose-ringed parakeet nest and was attacked by six parakeets, failed to hold on to the branches and fell to the pavement from a height of 12 meters.

Figure 1 – Instance of a black rat persecuted and attacked by a rose-ringed parakeet in Maria Luisa Park, Seville, May 25 2013. Darkness prevented a better-quality image (Photo: Dailos Hernández-Brito).

The number of observations as well as the time of the day at which they were recorded suggests that attacks by rose-ringed parakeets towards rats are not anecdotal, but rather a difficult to observe behavior. Our observations were mostly carried out during scheduled field-work aimed to assess interactions between rose-ringed parakeets and native avifauna (Hernández-Brito et al., 2014), so most attacks were recorded in the morning or early afternoon (Fig.2B). In the twilight hours, rose-ringed parakeets gather in large flocks and leave for the roost (Pithon and Dytham, 1999; Hernández-Brito and Luna, unpubl. observ.). Only breeder females stay in their nest over night when their pairs return to the communal roost in the breeding season (Butler, 2003). Therefore, we expect more attacks would have been recorded if our observations included the crepuscular period before parakeets return to the roost, given the nocturnal behavior of rats (Hooker and Innes, 1995; Cox et al., 2000).

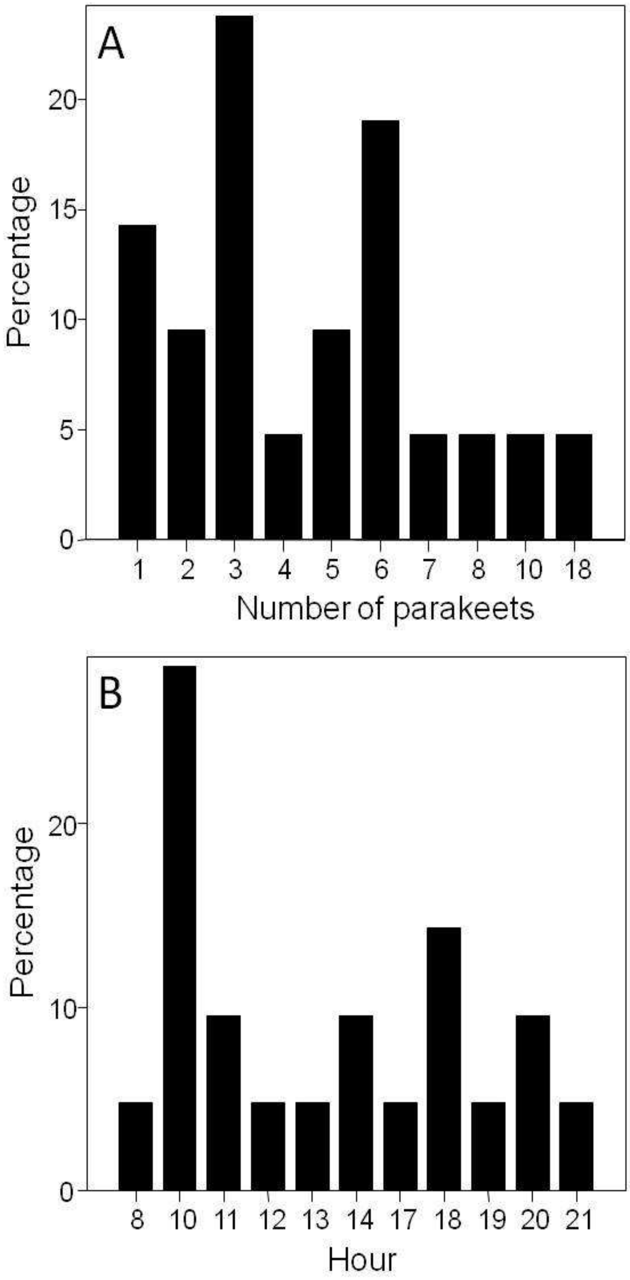

Figure 2 – Percentage of cases showing A) the number of rose-ringed parakeets involved in attacks on rats; and B) the time of day when attacks were recorded.

Rats (*Rattus* sp.) are often invasive predators, and their negative effects on native and endemic avifauna in oceanic islands are well known Atkinson (1985); Traveset et al. (2009). On the other hand, urbanization changes the abundance and richness of predator communities Chace andWalsh (2006), and thus rats can reach high population densities in the cities McKinney (2008). They can wipe out small populations of exotic parrots, as Scortecci (1953) recorded in the vicinity of a zoo in Italy, where a colony of monk parakeets (*Myiopsitta monachus*), the first established in this country (Spanò and Truffi, 1986), ceased to exist as a result of rat predation on parakeet eggs and chicks. At this point, and although we do not have direct evidence in the wild, black rats are potential predators of rose-ringed parakeet nests and even of adults (while incubating or sleeping, as has been recorded in captivity; J.L. Tella and M. Carrete, unpubl. observ.), so these aggressions may serve the same purpose as attacks on red squirrels, also known predators of parakeet nests (Mori et al., 2013). This aggressive behavior, along with the aggressiveness of rose-ringed parakeets towards avian predators, could explain why the nests of some bird species are aggregated in the proximity of nesting rose-ringed parakeets in Seville (Hernández-Brito et al., 2014). Although rose-ringed parakeets may displace (Hernández-Brito et al., 2014) and even kill coexisting bats, which compete for nesting cavities (Menchetti et al., 2014), other bird species may be favored by the antipredatory behavior of parakeets, thus increasing their breeding success. Three bird species (common blackbird *Turdus merula*, spotless starling *Sturnus unicolor* and collared dove *Streptopelia decaocto*) breeding in the proximity of rose-ringed parakeets joined the parakeets in chasing the rats in four cases. Together, these observations suggest that species benefit from other species' aggressiveness toward predators (e.g., Blanco and Tella, 1997), and indicate that the impact of rose-ringed parakeets on native fauna may be both negative and positive depending on the species considered and its conservation status (Hernández-Brito et al., 2014).

Despite the fact that non-native populations of rose-ringed parakeets have spread throughout at least 35 countries (Butler, 2003), research aimed to assess their impact on native fauna has focused mostly on birds and has centered on only a few European cities (Strubbe and Matthysen, 2007, 2009; Orchan et al., 2013; Hernández-Brito et al., 2014). More attention should be devoted to their interactions with more elusive mammals, such as rats and bats, with a widespread occurrence in cities worldwide.

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Chapter III

Nest-site competition and killing by invasive parakeets cause the decline of a threatened bat population

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ABSTRACT

The identification of effects of invasive species is challenging owing to their multifaceted impacts on native biota. Negative impacts are most often reflected in individual fitness rather than in population dynamics of native species and are less expected in low-biodiversity habitats, such as urban environments. We report the long-term effects of invasive rose-ringed parakeets on the largest known population of a threatened bat species, the greater noctule, located in an urban park. Both species share preferences for the same tree cavities for breeding. While the number of parakeet nests increased by a factor of 20 in 14 years, the number of trees occupied by noctules declined by 81%. Parakeets occupied most cavities previously used by noctules, and spatial analyses showed that noctules tried to avoid cavities close to parakeets. Parakeets were highly aggressive towards noctules, trying to occupy their cavities, often resulting in noctule death. This led to a dramatic population decline, but also an unusual aggregation of the occupied trees, probably disrupting the complex social behaviour of this bat species. These results indicate a strong impact through site displacement and killing of competitors, and highlight the need for long-term research to identify unexpected impacts that would otherwise be overlooked.

INTRODUCTION

Biological invasions are considered as one of the most serious threats to biodiversity worldwide owing to their impacts on native biota and ecosystem functioning (Simberloff et al. 2013). However, detecting and quantifying the effects of invasive species on native biodiversity can be challenging owing to the variety of potential, multifaceted impacts (Simberloff et al. 2013). For example, invasive bird species may impact native species through different mechanisms such as predation, competition, hybridization or disease propagation (Blackburn et al. 2009). Thus, significant research effort is required to assess each of these processes. Moreover, most research has focused on only a few invasive species. For example, the most recent review of studies on the impacts of invasive birds shows that published research focusing on potential impacts only exists for 18% of non-native bird species introduced worldwide (Martin-Albarracin et al. 2015).

The rose-ringed parakeet (*Psittacula krameri*) is one of the most studied invasive bird species, probably because it has established non-native populations worldwide (Butler 2003; Pârâu et al. 2016; Cardador et al. 2017) and is considered one of the 100 worst alien species in Europe (http://www.europe-aliens.org/speciesTheWorst.do). Thus, this species has been the subject of several reviews on ecological impacts (Menchetti and Mori 2014; Menchetti et al. 2016) and of systematic risk assessments (Carboneras et al. 2017; Turbé et al. 2017). Some studies have assessed the negative impacts of rose-ringed parakeets on native birds through competition for food in bird feeders, where parakeets disrupt the foraging behaviour of native birds (Peck et al. 2014; Le Louarn et al. 2016), and for nest sites of several cavity-nesting birds (Strubbe and Matthysen 2009; Orchan et al. 2013; Dodaro et al. 2014; Hernández-Brito et al. 2014a; Charter et al. 2016; Yosef et al. 2016; Mori et al. 2017). However, as in other invasive bird species for which information is available, these studies only indicate impacts on the individual fitness of native birds. More information is needed to properly assess impacts at a population level (Martin-Albarracin et al. 2015).

Some years ago, we reported an unexpected impact of rose-ringed parakeets (hereafter parakeets) on a threatened bat species, the greater noctule *(Nyctalus lasiopterus*, hereafter noctule) (Hernández-Brito et al. 2014a). This is the largest European bat species and is classified as Vulnerable on the IUCN Red List of Threatened Species (Alcalde et al. 2016). By 2003, the largest known European colony of this species was located in the María Luisa Park, an urban park located in Seville (southern Spain) where noctules used cavities of large trees as breeding sites and diurnal refuges. Ten years later (2013), we found several lines of evidence suggesting that the colonization of the park by invasive parakeets was having a negative impact on the noctule population: both species shared preferences for the same types of cavities, with noctules avoiding proximity to parakeets and parakeets occupying tree cavities previously used by noctules (Hernández-Brito et al. 2014a). Here, we provide a longer-term monitoring study (until 2017), showing a dramatic reduction in the number of trees used by noctules linked not only to interspecific competition for tree cavities but also to aggressions by parakeets resulting in the death of noctules.

MATERIAL AND METHODS

Study area and species

The María Luisa Park is situated in Seville, southern Spain (37°24′ N, 5°59′ W, altitude 10 m above sea level). With an area of approximately 40 ha, this park was established in 1850 and has dense vegetation, with large and old exotic trees (mainly *Platanus* sp., *Gleditsia triacanthos* and *Sophora japonica*) that offer numerous cavities for cavity-nesting species. There are no primary cavity-nesting species in this park (e.g. woodpeckers) that could excavate cavities, so all available cavities stem from tree decay. In addition, the land surrounding Seville is highly deforested and mostly devoted to agriculture, thus offering little habitat for forest-dwelling species.

The greater noctule has a very scattered distribution throughout central and southern Europe, and Spain constitutes the main core area for the species (Alcalde et al. 2016). This species shows spatial sexual segregation (Ibáñez et al. 2009) and, during the breeding season, females gather in small maternity colonies (Alcalde et al. 2016). The María Luisa Park was thought to hold the largest local population of this species, as earlier studies conducted in just a sector of the park roughly estimated the presence of 500 adults (mostly females) (Ibáñez et al. 2009). Females form fission–fusion societies, resulting in several differentiated maternity colonies that occupy several cavities in different trees, with an average of 27 females simultaneously sharing a tree cavity (Popa-Lisseanu et al. 2008; Fortuna et al. 2009). Females may use different trees across the reproductive season and thus each maternity colony may occupy a minimum of 30 trees with adequate cavities, with the number of females using a particular cavity changing over time (Popa-Lisseanu et al. 2008). Nonetheless, females show long-term fidelity to the same groups of trees (some trees had been used for at least 14 years; Popa-Lisseanu et al. 2008). Females usually arrive at the park in March, giving birth to one or two pups in May–June. Although most of them leave the park from August to November, others stay year round (Popa-Lisseanu et al. 2008; Ibáñez et al. 2009). They have large foraging ranges, usually moving 15–40 km from the park in a single night to hunt insects and migrating songbirds (Popa-Lisseanu et al. 2009). Their annual survival rates were similar to those of other long-distance aerial-hawking bat species (Papadatou et al. 2012). Genetically, this population is closely related to the two closest colonies of the species found in Jerez de la Frontera and Doñana National Park (Santos et al. 2016), located 60 km and 75 km from María Luisa Park, respectively.

The rose-ringed parakeet is a successful invader in Europe. Their success is a result of the large numbers of individuals imported as cage birds, frequent accidental escapes or deliberated releases and niche similarity between areas of introduction and their native Asian habitats (Cardador et al. 2016; Abellán et al. 2017). The first introduction in Seville most probably occurred in 1992 with a very small group of individuals deliberately released in María Luisa Park. This is a highly sociable species that nests in cavities (mostly in trees but also in buildings; Hernández-Brito et al. 2014a) and produces one to four offspring per year. In María Luisa Park, most parakeets select tree cavities for nesting between late December and February and lay eggs mostly in March. There is, however, large variation in breeding phenology among pairs, with fledglings leaving the nests between May and early July. Moreover, newly formed immature pairs and groups of non-breeding individuals inspect and use tree cavities throughout the breeding season.

Another eight cavity-nesting bird species are breeding in María Luisa Park (Hernández-Brito et al. 2014a). However, we have previously shown that the only species competing with noctules for tree cavities was the rose-ringed parakeet (Hernández-Brito et al. 2014a). Thus, the rest of the species were not considered in this study.

Population monitoring

Although our first studies on noctules in María Luisa Park date back to 1992 (Popa-Lisseanu et al. 2008), it was not until 2003 that we geolocated all trees used by the species in a single year. Unfortunately, we were not able to obtain a census of the whole adult population of noctules. Obtaining accurate population sizes of forest bats forming fission–fusion societies, such as the greater noctule, is extremely difficult (Hayes et al. 2009; Kunz et al. 2009). In fact, there is no published information on population sizes for this or similar bat species. Therefore, we relied on temporal changes in the number of trees used by the species as a surrogate of changes in population size. We did not know the breeding population size of parakeets in 2003 as the species was still very scarce and little attention was paid to it because no impacts were expected at that time. We can, however, obtain a reliable estimate of the number of parakeet nests in 2003 from a demographic model built with the year of the first introduction, detailed population counts conducted since 2011 and breeding parameters obtained from the same population (Carrete et al. in prep.).

In 2013 and 2016–2017, we simultaneously took a census of the number of nests of parakeets and the number of trees used by noctules in the park. Our monitoring programme extended from January to early August (covering the breeding season of both species), and observations were conducted in the morning (08.00–12.00 h) and afternoon (17.00–21.00 h). We GPS-located (±3 m) each year all tree cavities that we were able to visually inspect using 10 × 50 binoculars. We visually estimated the height of the cavity above ground (in m) and the width of its entrance (in cm), which was scored as small, medium or large (less than 4 cm, 4–8 cm and greater than 8 cm, respectively) (Hernández-Brito et al. 2014a). We did not consider the orientation of the cavities (Hernández-Brito et al. 2014a), as in other studies on nest-site competition between parakeets and native species (Orchan et al. 2013; Dodaro et al. 2014; Charter et al. 2016; Yosef et al. 2016; Mori et al. 2017), because orientation did not affect the selection of cavities in a previous study (Strubbe and Matthysen 2009). Our previous analyses showed a preference of both parakeets and noctules for cavities well above ground (approx. 15 m) and with medium-sized entrances (Hernández-Brito et al. 2014a). Thereafter, we repeatedly visited and observed at a distance (for a minimum of 10 min) each cavity on at least 10 different days evenly spaced throughout the breeding season of the two species. Given that parakeets can enter cavities that are not used as nests (see above), we conservatively considered as active parakeet nests those cavities where we observed adults entering a minimum of 10 times on different days, heard chicks inside or observed juveniles at the entrance. Regarding the identification of trees used by noctules, we complemented the previous methodology for monitoring tree cavities with the use of an ultrasound bat detector (Pettersson D230) and systematic observations at sunset to observe noctules leaving tree cavities (Hernández-Brito et al. 2014a).

Aggressive interactions

Interactions between parakeets and noctules were observed during the monitoring activities described above. When we observed harassment and attacks of parakeets towards noctules present inside or in the entrance of their tree cavities, we recorded the duration of the aggression (in minutes), whether the noctule was expulsed and whether the parakeet later entered the cavity. Dead and injured noctules were also found, always under trees occupied by noctules. After unexpectedly encountering the first case of a dead noctule, we proceeded to record these events more systematically. We are convinced that many cases were overlooked because dead and injured noctules could be hidden by ground vegetation, scavenged by cats and rats or, as we later learned, recovered by people working in the park or visitors. The corpses we found were transported to the laboratory for a detailed visual examination of damage to the skin and bones.

Spatial arrangement of noctules

Each year (2013, 2016 and 2017) we geolocated the cavities used by parakeets and noctules as well as those that remained unoccupied. The occupancy of a particular tree cavity by noctules could be influenced by the availability of unoccupied cavities as well as by the spatial distribution of cavities occupied by the same and/or other species, driven not only by competition but also by conspecific attraction processes (Hernández-Brito et al. 2014a). We thus measured the Euclidean distance from each cavity to the nearest cavity occupied by noctules and parakeets (nearest-neighbour distance) as well as the corresponding aggregation indexes. Aggregation indexes were obtained as the relative position of each cavity within the whole distribution of all cavities occupied by conspecifics or heterospecifics using $\Sigma\exp(-d_{ij})$, with ($i \neq j$), where d_{ij} is the linear distance between cavities i and j, and j represents all occupied cavities (Moilanen and Hanski 1998). Nearest-neighbour distances and aggregation indexes are complementary and depict the social environment around each cavity at a landscape scale as well as the existence of close conspecifics and competitors in its proximity (Hernández-Brito et al. 2014a). The two main sources of habitat heterogeneity in our study area, i.e. the proximity to surrounding streets and forest cover, were not considered because our previous work showed no effects on the spatial arrangement of noctules and parakeets (Hernández-Brito et al. 2014a).

We employed generalized linear models (GLMs) with a binomial error distribution and logistic-link function to ascertain factors explaining the probability of occupation of a cavity by noctules, fitting as explanatory variables its traits (entrance size and height above ground) and its nearest distance and aggregation to both noctules and parakeets. As values of nearest distance and aggregation for the same species were highly correlated (all $p < 0.001$), we alternatively included in models only one of these spatial descriptors. Continuous variables were standardized for modelling. Models were separately built for the most distant years (2013 and 2017) from which we gathered spatial information from both species, using the Akaike information criterion corrected for small sample sizes (AICc) for model selection (Burnham and Anderson 2002). Within each set of candidate models, we calculated ΔAICc*i* as the difference between the AICc of model *i* and that of the best-supported model (i.e. the model with the lowest AICc). Models within 2 AICc units of the best supporting model were considered as alternatives. We also quantified the plausibility of each model as being the best approximation using Akaike weights, *w* (Burnham and Anderson 2002), and performed model averaging (MuMIn package) to estimate the relative importance of all variables through the calculation of model-averaged estimates and confidence intervals (CIs) using the set of alternative models. A given effect received no, weak or strong support when the 95% CI for the coefficient estimate strongly overlapped zero, barely overlapped zero or did not overlap zero, respectively. We calculated the percentage of deviance explained by the best-supported models, obtained as 100 − (deviance of model *i*/deviance null model) * 100), for assessing their goodness of fit. All statistical analyses were conducted in R v. 3.1.2 (R Core Team 2013), and raw data used for analyses are provided in the electronic supplementary material.

RESULTS

Interspecific aggressions

During the breeding seasons of 2016 and 2017, we recorded 36 aggressions of parakeets towards noctules in trees occupied by both species. Most aggressions (55.6%) were recorded in May and during the 3 h before sunset (83.3% of aggressions). All of these aggressions happened at the entrance of tree cavities, and in 16 cases, we observed parakeets attacking noctules with their beaks while emitting loud sounds (figure 1). These aggressions usually lasted from 1 to 25 min, reaching in one case up to 145 min (median: 13.13 min), and ended with the parakeets entering the tree cavity after the attacked noctule was expulsed and obliged to flee during the daytime. Once parakeets entered the tree cavity, we were not able to observe whether or not they attacked other noctules that may have been inside the cavity. In 20 other instances, parakeets ceased their aggression and left the tree at sunset without successfully expelling the noctules from their refuge cavities.

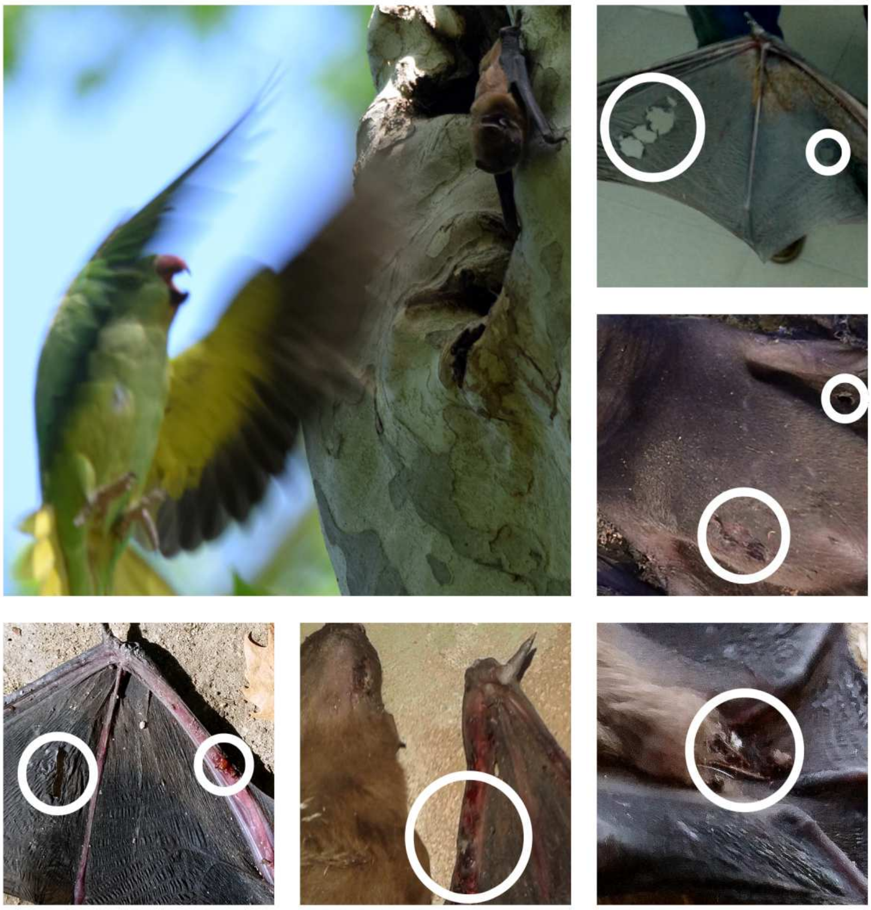

Figure 1. Main picture: an adult female rose-ringed parakeet attacks a greater noctule at the entrance of a tree cavity used as a refuge by noctules in María Luisa Park, Seville, on 17 May 2016. One noctule was found dead under the same tree the next day, with wounds caused by parakeets. Accompanying pictures: details of different types of wounds caused by parakeets on noctules found dead under their tree refuges (photographs: Dailos Hernández-Brito).

During the same period, we found 20 dead and two injured noctules under 18 different trees, all of them with active nests of parakeets. Seven of these noctules were found dead under the same tree where we recorded aggressions by parakeets the previous day. Dead noctules included three few-day-old pups, 10 lactating young and seven adults, as well as one pregnant female. Eight of these corpses were too putrefied to allow us to observe wounds or other indications of attack (temperatures reached 33–40°C during the study period, so corpses decomposed rapidly). The other 12 corpses were fresh enough to show clear wounds caused by the beaks of parakeets (figure 1). These wounds were present mainly on the wings, consisting of holes in the membranes (dactylopatagium and plagiopatagium areas), chafing on the skin covering the phalanges and forearm, breakages of phalanges, and wounds both on the upper side of the body and the abdomen. The two injured, but still living adult noctules showed similar wounds and were not able to fly or to climb the trunks of trees to return to their cavity refuges. We suspect that noctules were injured and killed when parakeets entered their cavities after expelling other noctules (see above), because pups and lactating young do not leave the cavities. We did not observe aggressions addressed to noctules by other species, neither did we find evidence of other species preying on or killing noctules in the park.

Temporal trends in the occupation of trees

Figure 2 shows the numbers of nests of parakeets and trees occupied by noctules in María Luisa Park from 2003 to 2017. Parakeets were scarce in this area in 2003 and, although we did not conduct a detailed census, our demographic-based estimation suggests that the local breeding population would have been as low as 13 nests at that time. Three annual detailed censuses conducted since 2013 showed an increase to 311 active nests in 2017 (figure 2). This means a 96% population increase from 2013 to 2017, and an estimated 2192% population increases from 2003 to 2017. Noctules showed an opposite trend: cavities used as refuges were found in 75 trees in 2003, the number decreasing to only 14 trees in 2017 (figure 2). This resulted in a 70% decrease between 2013 and 2017, and an 81% decrease between 2003 and 2017.

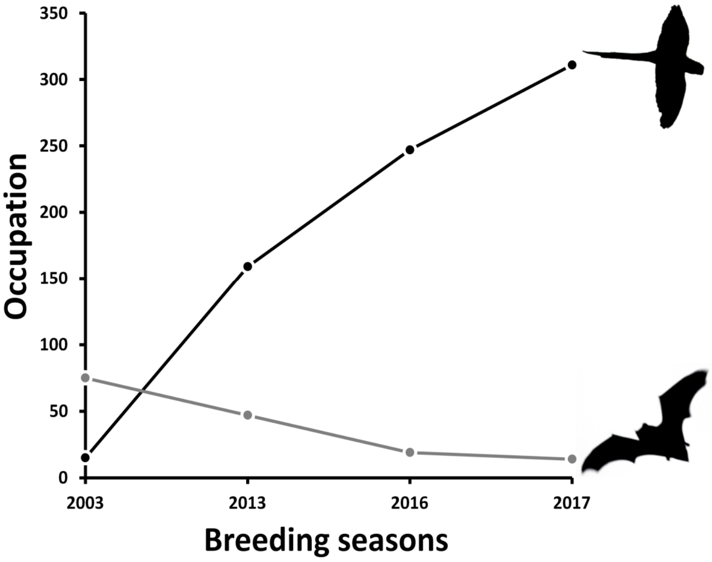

Figure 2. Changes in the number of nests of rose-ringed parakeets and trees occupied by greater noctules across years in María Luisa Park.

Spatial segregation between noctules and parakeets

Figure 3 shows the spatial distribution of parakeet nests and noctule refuges recorded across years in the park, indicating not only a reduction in the number but also a spatial contraction of noctule refuges along with an increase and spatial expansion in parakeet nests. In 2013, the first year we recorded both noctule refuges (n = 47 trees) and parakeet nests (n = 159 nests) (figure 3), the best-supported model indicates that the probability a tree cavity was occupied by noctules was related to its entrance size and height above ground and to the nearest distances to other noctule refuges and parakeet nests (table 1). In this year, noctules used cavities well above ground level and with medium- to large-size entrances, close to other noctule refuges and far from the nearest parakeet nest (table 2). In 2017, when the number of trees occupied by noctules had declined to 14 while the number of parakeet nests had increased to 311 (figure 3), the four alternative models obtained for the probability of occupation of cavities by noctules also included variables describing the characteristics of the cavity as well as the descriptors of the presence of parakeet and noctules in the surrounding area (table 1). However, after model averaging, the only variable receiving strong support was the distance to the nearest parakeet nest (table 2). Thus, the probability of occupancy of a cavity by noctules was higher than expected at short distances to parakeet nests. These results suggest that in 2017, noctules were forced to use cavities at any height above ground or size, being unable to avoid close proximity to some parakeet nests (most of the trees used also held a parakeet nest; see below).

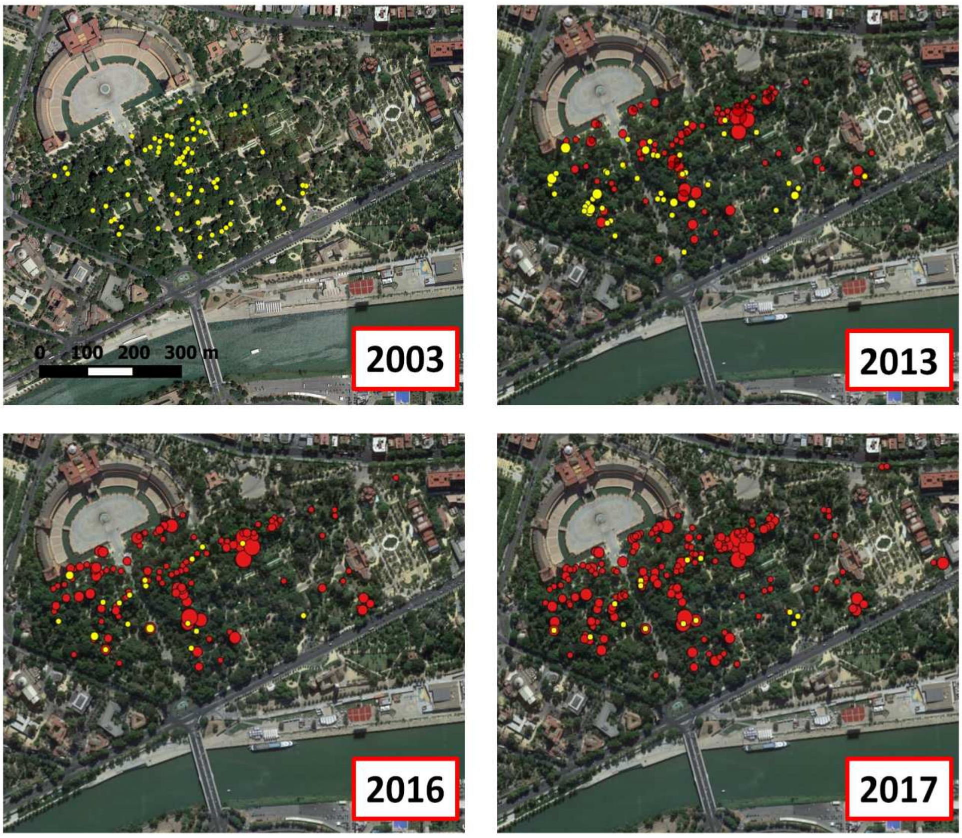

Figure 3. Distribution of trees with refuges of greater noctules (yellow dots) and with nests of rose-ringed parakeets (red dots) in María Luisa Park across years. Larger dots indicate overlapping points.

Table 1. GLMs obtained to explain the probability of occupancy of tree cavities by greater noctules in María Luisa Park, Seville, in 2013 and 2017. (Explanatory variables reflect the size of the cavity entrance (size; small size taken as reference), the height above ground of the cavity entrance (height), the distance to the nearest noctule refuge (nndn) or parakeet nest (nndk) and the aggregation of noctule refuges (agregn) and parakeet nests (agregk) around each cavity. Only the 10 first models, after ranking using AICc, are shown (null models were ranked 34th and 21st for 2013 and 2017, respectively). Models with ΔAICc less than or equal to 2 were considered as alternative (in italics). K: number of parameters; AICc: Akaike information criterion corrected for small sample sizes; ΔAICc: difference between the AICc of model i and that of the best-supported model (i.e. the model with the lowest AICc); weight: Akaike weights; %dev: deviance explained by alternative models.)

Models 2013	**k**	**AIC**	**ΔAICc**	**weight**	**%dev**
size, height, nndk, nndn	6	302.7	0	0.79	22.61
size, height, agregk, nndn	6	306.1	3.38	0.15	
size, height, nndn	5	307.9	5.16	0.06	
height, nndk, nndn	4	314.9	12.13	0.00	
height, agregk, nndn	4	317.2	14.48	0.00	
size, nndk, nndn	5	318.2	15.5	0.00	
size, agregk, nndn	5	319.5	16.7	0.00	
height, nndn	3	319.5	16.8	0.00	
size, nndn	4	320.5	17.74	0.00	
agregk, nndn	3	332	29.2	0.00	
Models 2017	**k**	**AIC**	**ΔAICc**	**weight**	**%dev**
size, nndk	4	124.9	0	0.33	17.76
size, nndk, agregn	5	125.5	0.58	0.24	18.79
size, height, nndk	5	125.9	0.96	0.20	18.52
size, height, nndk, agregn	6	126.6	1.66	0.14	19.47
nndk	2	129.3	4.42	0.04	
nndk, agregn	3	130.4	5.46	0.02	
height, nndk	3	130.6	5.72	0.03	
height, nndk, agregn	4	131.8	6.87	0.01	
size, height, agregn	5	137.7	12.8	0.00	
size, height	4	138.1	13.16	0.00	

Table 2. Variables explaining the probability of occupancy of tree cavities by greater noctules in María Luisa Park, Seville, in 2013 and 2017. (Averaged estimates and 95% CIs (2.5% and 97.5%) were obtained from the best-supported models (ΔAICc less than or equal to 2, table 1). The effect of a given variable has no, weak or strong support when the 95% CI strongly overlapped zero, barely overlapped zero or did not overlap zero, respectively. Table 1 gives abbreviations of variables.)

Variables	Estimate	2.50%	97.50%
2013			
Intercept	-5.90	-7.58	-4.58
medium size	1.89	0.8	3.35
large size	2.06	0.89	3.56
height	0.62	0.33	0.92
nndk	0.62	0.17	1.06
nndn	-3.11	-4.51	-1.91
2017			
Intercept	-1.71	-23.85	20.42
medium size	1.37	-0.82	3.56
large size	2.26	-0.18	4.70
nndk	-4.74	-8.82	-0.66
agregn	5.65	-14.67	25.97
height	0.09	-0.28	0.46
agregk	0.00	-0.10	0.10

The occupancy of trees by noctules may also be related to temporal changes in the availability of trees with adequate cavities because of tree decay and management of the park by public garden authorities. However, our previous results showed that 49 of the trees occupied by noctules in 2003 were unoccupied in 2013 by this species, despite the fact that they still had cavities (which were occupied by parakeets in almost half of the cases), and that the probability of tree abandonment was positively related to the presence of parakeet nests in the same tree and to the aggregation of parakeet nests around the tree (see Hernández-Brito et al. 2014a for statistical analyses). Only two of the 47 trees occupied by noctules (4.25%) in 2013 were also occupied by parakeets. In 2017, 38 trees previously occupied by noctules were unoccupied by this species but occupied by parakeets. In contrast to 2013, 11 of the 14 trees occupied by noctules (78.6%) were also occupied by parakeet nests.

DISCUSSION

Detecting the negative effects of invasive species on native biodiversity is challenging. While threats to endangered, endemic or charismatic species generally attract attention, gradual changes in abundance and distribution of common species tend to pass unnoted (Simberloff et al. 2013). Moreover, little attention has been paid to the potential impacts of non-native species invading urban environments because it is often assumed that these habitats hold low biodiversity, which is mainly represented by common, widespread human commensal species, leaving vacant niches for invaders (Sol et al. 2017). Here, we demonstrate a process by which an invasive bird species, mostly occupying urban environments (Abellán et al. 2017), impact a threatened bat species. These impacts would have passed unnoted if the bat population had not been monitored 14 years ago, previous to the spread of the invader.

Our results, together with previous knowledge on the behavioural ecology of this population of noctules, allow us to hypothesize that a temporal process exists in their interactions with parakeets. The long-term monitoring (1992–2006) of transponder-equipped and radio-tagged noctules showed that they returned year after year to the park, forming a complex fission–fusion society. Females often switched roosting trees but differentiated maternity colonies remained constant both spatially and across years (Popa-Lisseanu et al. 2008; Fortuna et al. 2009). On the other hand, parakeets are highly aggressive against other cavity-nesting species and even against predators of much larger size, winning most of the aggressive encounters that we have recorded (Hernández-Brito et al. 2014a). Thus, during the first 10 years of this study (2003–2013), the slow but progressive increase in parakeet numbers may have caused an increase in the number of noctule cavities occupied by parakeets when noctules arrived at the park in March. In addition, some noctules were actively expulsed from their cavities by parakeets. This surely forced noctules to look for alternative cavities far from the trees occupied by parakeets. By 2013, the number of trees occupied by noctules was reduced by 30%, and these trees were spatially aggregated and segregated from the proximity of parakeet nests. There is the possibility that some noctules dispersed to other colonies owing to the progressive scarcity of tree cavities and harassment by parakeets. The two closest colonies are located in Doñana National Park and Jerez de la Frontera, 60 and 77 km from María Luisa Park, holding a maximum of 40 and 150–200 individuals across years, respectively. Although genetic studies showed no differentiation between these colonies (Santos et al. 2016), our long-term monitoring of the three colonies does not support this idea. While many of the more than 300 females marked in María Luisa Park were recaptured within the same park across years (Popa-Lisseanu et al. 2008), only one of these females visited Doñana (in 2001, 2003 and 2004), while two females marked in Doñana and Jerez visited María Luisa Park (2007 and 2017) and three females marked in Jerez visited Doñana (2004–2016), all for short periods of time. These data indicate that contacts between colonies seem to be occasional and performed by very few individuals. In addition, the decrease of the María Luisa Park population was not paralleled by any drastic increase in the other two colonies. A further population increase in parakeets would have led to a greater reduction and spatial contraction of noctule tree refuges in María Luisa Park. By 2017, the number of cavities not used by parakeets could have been so low that noctules were forced to use any available cavity in trees that hold parakeet nests, in almost 80% of cases. It is worth noting that the deviance explained by occupancy models was relatively low (table 2), probably because many of the unoccupied cavities included in the statistical analyses could be, in fact, unsuitable for the species. (We could not inspect the interior of unoccupied cavities and thus we did not know whether they were large enough to hold parakeet nests and noctule refuges.) This extreme competition for tree cavities and the close proximity of parakeet nests could explain the aggressive attacks and killing of noctules by parakeets recorded in 2016–2017. However, many dead noctules could have passed unnoted (see Material and methods), and these aggressions may have been overlooked in the past. In fact, an aggression had been reported in 2005 (cited in Hernández-Brito et al. 2014a), and several people working in María Luisa Park spontaneously told us in 2016 that they frequently observed aggressions by parakeets and recovered dead and injured noctules in past years. Therefore, it seems that aggressions and fatal attacks do not constitute a recent phenomenon but perhaps increased in frequency and intensity as a result of the increased competition for cavities, thus making observation more likely by researchers.

In contrast with a recent review of impacts by invasive bird species (Martin-Albarracin et al. 2015), our results indicate an impact not only on individual fitness of native fauna (i.e. through nest-site usurpation and displacement to presumably poorer sites) but also at the population level, which has been thus far poorly studied. Greater noctules, weighing approximately 50 g, are unique because they are the only bat species in Europe that are able to hunt small passerine birds (usually less than 25 g) while they are migrating at night at long distances from their maternity colonies (Ibáñez et al. 2001, 2016). However, noctules do not seem to be able to survive the attacks of the much larger and more powerful parakeets (weighing approx. 120 g, figure 1). In fact, parakeets have been observed killing other bird (Covas et al. 2017) and bat species (Menchetti et al. 2014), and even rats (Hernández-Brito et al. 2014b). Therefore, the 81% reduction in the number of trees occupied by noctules in 14 years seems to be the result of both site displacement and direct mortality caused by parakeets. Bats are long-lived species with slow reproduction rates, and thus, their ability to compensate for high predation rates is very limited (Barclay and Harder 2003). Moreover, the annual survival rates of noctules living in María Luisa Park before the population growth of parakeets was low (0.74) compared to other forest bat species that forage at shorter distances (Papadatou et al. 2012). Therefore, an increment in mortality rates caused by parakeets both on lactating and adult noctules would severely affect the population dynamics of this population and contribute to its dramatic decline. Unfortunately, we were unable to measure temporal changes in population size owing to the methodological difficulties of accurately estimating population sizes of forest bat species that form fission–fusion societies (Hayes et al. 2009; Kunz et al. 2009). However, it is reasonably expected that the population size would have declined in parallel with the 81% reduction in the number of tree cavities used. Population size, as well as social structure, is expected to be affected: females were originally distributed across the park forming differentiated, stable maternity colonies (Popa-Lisseanu et al. 2008; Fortuna et al. 2009; figure 3), something certainly disrupted given the scarcity and aggregation of the trees currently used (figure 3). This social disruption may have unexpected effects on the breeding biology of the species.

Actions to reduce the population of parakeets and to provide artificial refuges for noctules are urgently needed. Without that, this population, which was once the largest known for this threatened bat species in its range (Fortuna et al. 2009), could be completely extinct within a few years. The provision of artificial refuges alone would be insufficient, given that noctules learn to use them slowly (C. Ibáñez 2003, unpublished data) and that the population size and direct impacts of parakeets are increasing at a much faster rate. An eradication plan of parakeets was planned for early 2017 by the city government of Seville, but this was cancelled owing to pressures by animal welfare associations, even though it was supported by a Spanish law which specifically deals with the management of invasive species (Real Decreto 630/2013). Programmes for the control or eradication of invasive species often face public opposition (Blackburn et al. 2010), especially when dealing with charismatic species such as parakeets (Carrete and Tella 2008).

Our work exemplifies the challenges in understanding the true ecological impacts of invasive birds. While the number of introduced non-native bird species increases worldwide (Dyer et al. 2017) and invasion risks increase in new regions (Cardador et al. 2017), the scientific community is only able to study a small fraction of these populations and their multifaceted potential impacts (Martin-Albarracin et al. 2015). Moreover, some impacts, such as those reported here, are unexpected and can be easily overlooked in the absence of long-term research. In this sense, we speculate whether other impacts on bats remain hidden. Many European bat species, some of them threatened, are closely linked to buildings and urban habitats (Ancillotto et al. 2015; Russo and Ancillotto 2015; Rydell et al. 2017)); meanwhile, parakeets are spreading across European cities (Cardador et al. 2016; Abellán et al. 2017). There is concern that parakeets could reduce the availability of suitable tree cavities for the noctule bat (*Nyctalus noctula*) in the Netherlands (Haarsma and van der Graaf 2013). One Leisler's bat (*Nyctalus leisleri*) was found killed by parakeets in Italy (Menchetti et al. 2014), and parakeets seem to be competing for greater noctule refuges in Jerez de la Frontera (I. Sánchez and D. Hernández-Brito 2017, personal observation). Parakeets can also compete for cavities in buildings that they use for nesting, which can be usurped from other bird (Hernández-Brito et al. 2014a) and bat species. One of the authors (D. Hernández-Brito) observed in Seville, on 7 July 2017, three parakeets attempting to force isabelline serotine bats (*Eptesicus isabellinus*) out from a wall cavity in a tall building during the daytime. Seventy-eight bats later flew out from that cavity at sunset.

All of these observations can be considered as anecdotal and do not necessarily imply an impact on bat populations. Similarly, the first observation of parakeets harassing a noctule in María Luisa Park in 2005 (Hernández-Brito et al. 2014a) would not have indicated a population impact until the long-term research presented here. As a matter of concern, a recent meta-analysis shows that large impacts caused by invasive species can often be missed owing to small sample sizes, resulting in high Type II error rates and false certainty of no impact (Davidson and Hewitt 2014). Therefore, much more research is needed to properly assess the impact of parakeets and other invasive species on a variety of bat species (Welc and Leppanen 2017).

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SUPPLEMENTARY MATERIAL

Appendix S1. (*see Supplementary Material Section 1-Chapter III*).

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SECTION 2:

NOVEL INTERACTIONS AGAINST BIOTIC BARRIES

Chapter V

A protective nesting association with native species counteracts biotic resistance for the spread of an invasive parakeet from urban into rural habitats

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ABSTRACT

Non-native species are often introduced in cities, where they take advantage of microclimatic conditions, resources provided by humans, and competitor/predator release to establish and proliferate. However, native communities in the surrounding rural or natural areas usually halt their spread through biotic resistance, mainly via top-down regulative processes (predation pressure). Here, we show an unusual commensal interaction between exotic and native bird species that favours the spread of the former from urban to rural habitats.We show how Monk parakeets Myiopsitta monachus, an invasive species often introduced in cities worldwide, associated for breeding with a much larger, native species (the white stork Ciconia ciconia) to reduce predation risk in central Spain, thus allowing their colonization of rural areas. Parakeets selected stork nests close to conspecifics and where breeding raptors were less abundant. Parakeets always flushed when raptors approached their nests when breeding alone, but stayed at their nests when breeding in association with storks. Moreover, when storks abandoned a nest, parakeets abandoned it in the following year, suggesting that storks actually confer protection against predators. Our results show how a protective-nesting association between invasive and native species can counteract biotic resistance to allow the spread of an invasive species across non-urban habitats, where they may become crop pests. Monk parakeet populations are now growing exponentially in several cities in several Mediterranean countries, where they coexist with white storks. Therefore, management plans should consider this risk of spread into rural areas and favour native predators as potential biological controllers.

INTRODUCTION

Cities are often the first point of introduction for many alien species (Padayachee et al. 2017), some of which can take advantage of microclimatic conditions (Collins et al. 2000), resources provided by humans (Kark et al. 2007), or competitor or/and predator release (Gering and Blair 1999; Alberti 2015) to establish and proliferate. Thus, cities have become hotspots of invasive species (Gaertner et al. 2017), which can secondarily spread into nearby, rural landscapes (e.g. Alston and Richardson 2006; von der Lippe and Kowarik 2008; Marco et al. 2010; Abellán et al. 2017). However, native communities in the areas surrounding urban cores usually halt the spread of non-native species through biotic resistance (Catford et al. 2009), which may arise through competition (Foelker et al. 2003; Vilà and Weiner 2004; Strauss et al. 2006) but also via top-down regulative processes such as predation (Robinson and Wellborn 1988; Reusch 1998; Byers 2002; de Rivera et al. 2005).

Several studies have shown that predators can limit local population size or habitat use of invaders (Suter 1982; Robinson and Wellborn 1988; Reusch 1998; Byers 2002; Carlsson et al. 2009), although results are not conclusive. For instance, in some systems, native predators prey minimally on invaders (Trowbridge 1995) while in others, even if predators heavily prey on an invader, they have little overall influence on its success due to life history characteristics that compensate for high predation rates (Reusch 1998). In other cases, the variable influence of predators on invasion success may be due to facilitative interactions among invasive and native species (Ruesink 2007; Wright et al. 2018) or to habitat heterogeneity, which can create refuges where invasive species experience relaxed predation (Gause 1932; Menge and Sutherland 1976; Malmqvist and Sackmann 1996; Chalcraft and Andrews 1999; Leonard 2000; Byers 2002).

Interspecific protective associations are both facilitative interactions and a form of refuge where individuals of one species exploit the antipredatory behaviour of another relatively aggressive species to reduce predation risk (Quinn and Ueta 2008). These associations allow individuals to occupy habitats that are otherwise unsuitable because of the negative effects of predation (Prop and Quinn 2003; Quinn et al. 2003), increasing the realised niche of a species (Bruno et al. 2003). Despite the existence of several examples about facilitative interactions favouring invasive plants and invertebrates (Richardson et al. 2000; Altieri et al. 2010; Northfield et al. 2018), as well as positive effects of habitat refugees on invasion success (Phoebe et al. 2013; Wright et al. 2016), to our knowledge, no studies are testing the effect of interspecific protective interactions on invasion success.

Here, we explore the role of interspecific protective nesting interactions in facilitating the spread of an urban invasive avian species, the monk parakeet (*Myiopsitta monachus*), into neighbouring rural areas. The monk parakeet is one of the most widespread avian invaders, with invasive populations mainly in North America and Western Europe, but also in Asia, Africa and some oceanic islands (Strubbe and Matthysen 2009). This species has spread due to the international trade of millions of wild-caught parakeets from their native South American range (Carrete and Tella 2008; Edelaar et al. 2015; Cardador et al. 2017) to pet shops and homes across the globe. Posterior accidental escapes or releases have founded several invasive populations in urban habitats (Van Bael and Pruett-Jones 1996; Strubbe and Matthysen 2007; Abellán et al. 2016, 2017; Hobson et al. 2017). The fact that most of the non-native populations are urban may be explained by predation release, which allows a higher breeding success in their invaded urbanised habitats than in their native ranges, as was also shown for the highly invasive rose-ringed parakeet *Psittacula krameri* (Shwartz et al.

2009). In fact, recent work has demonstrated that the breeding success of monk parakeets is twice as high in a Spanish city than in its native range (Senar et al. 2016). Other hypotheses, such as competition or parasite release, seem unlike to explain the high success of monk parakeets in urban areas. Contrarily to the secondary cavity-nesting rose-ringed parakeet, which competes with native species for nest holes (Hernández-Brito et al. 2014), monk parakeets are unique among parrots as they build their own nests using wood sticks on trees and artificial substrates such as power pylons and roofs (Minor et al. 2012; Senar et al. 2019), thus avoiding competition for nest sites. Regarding parasite release, monk parakeets gain novel parasites from the recipient community in its invaded range while also maintain parasites from its native range (Mori et al. 2015; Ancillotto et al. 2018; Briceño et al. 2019).

Contrasting to their general urban habits in invaded regions, the largest Spanish population of monk parakeets (located in Madrid) has spread into the nearby rural area in recent years, in association with the massive nest structures of white storks *Ciconia ciconia* (Fig. 1). Previous studies show that, in its native range, monk parakeets can also build their nests associated with the nests of other stork species such as jabirus Jabiru mycteria (Burger and Gochfeld 2005). In the surroundings of Madrid, parakeets build their nests associated with nests occupied by breeding white storks. Despite parakeets can steal nest material from conspecific neighbours (Eberhard 1998; Bocheński and Jerzak 2006), we have never recorded cases of parakeets stealing sticks -to storks, may be due to of differences in the size and ductility of building materials for each species. Although nesting site availability does not explain the use of stork nests, as monk parakeets may use a variety of nesting substrates (Moreira-Arce et al. 2014; Senar et al. 2019), this association may confer breeding advantages to parakeets (Burger and Gochfeld 2005). Several small-sized native bird species such as sparrows and starlings are also tolerated by white storks and use their nests as nesting substrates (Indykiewicz 2006). The large-bodied white stork has extremely low nest predation rates, as learned from long-term breeding monitoring programs in Spain (e.g.; Baos et al. 2012; Vergara et al. 2006), and predation of adults is anecdotal (Tobolka 2014). Therefore, smaller bird species may also associate with white storks to reduce predation risk (Bocheński 2005; Kosicki et al. 2007), as it has been demonstrated for other protective nesting associations (Quinn and Ueta 2008).

Fig. 1 Parakeets and storks. Nests of monk parakeets (yellow arrows) associated with white stork nests. (Photos: D. Hernández-Brito)

Here, we hypothesised that monk parakeets associate with storks not because of structural benefits but to obtain protection against predation, thus allowing their spread into rural habitats despite the existence of a large predator community. To test this hypothesis, we first compared the probability of parakeet-stork associations between rural and urban habitats, predicting that they should be more frequent in the former, where predators are more abundant than in the latter. We then assessed whether these associations occur at random, or if they can be explained by a combination of biotic and abiotic factors such as the proximity of the stork nest to another parakeet colony (conspecific density), the type of substrate (pylons, trees, or roofs), or the density of predators in the surroundings (predation risk). We predicted that besides proximity to conspecifics, parakeets should breed preferentially in stork nests sited in pylons (thus reducing predation risk at the nest) in areas with a low density of aerial predators (thus reducing predation risk while foraging). The low density of predators in the surrounding of a nest ensures safe areas for parakeets to perform basic activities such as foraging. Nests in pylons, contrary to those located in trees or on roofs, are not accessible to mammalian or reptilian predators (Bocheński 2005), so the antipredatory effect of nesting with a stork is focused on aerial predators (i.e., raptors) and, thus, maximised. Finally, to discard the potential benefits derived from the nest structure per se, we evaluated the effect of nest abandonment by storks on the subsequent nest abandonment by parakeets. We predict that parakeets should abandon their nests after stork abandonment due to the disappearance of its protective effect against predators; otherwise, parakeets could associate with storks to simply take advantage of their nest structures. Complementarily, we compared the behaviour of parakeets toward approaching avian predators when breeding in association with storks or not. We predicted that parakeets should flush more frequently from raptors when breeding alone than when breeding with storks, where they can take advantage of the presence of the protective species, which can deter raptor attacks.

MATERIAL AND METHODS

Study area and fieldwork

The study was carried out in an extensive area including the city of Madrid and its surrounding rural habitats along the Manzanares and Jarama rivers (Fig. (Fig.2),2), an area mostly devoted to irrigated, intensive agriculture (mainly maize and vegetables) and gravel extraction. In this area, raptors nest mostly in riparian forests, while white storks nest in the same forest as well as on electric pylons and building roofs (Blanco 1994; 1996).

During the breeding seasons (April–August) of 2014 and 2015, the study area was repeatedly visited to GPS-locate all nests of parakeets and storks present in the urban and rural habitats (Fig. (Fig.2),2), also recording the type of substrate in which the nests were located (tree, pylon or roof). Moreover, we monitored the community of medium-sized raptor species present in the study area, including the black kite *Milvus migrans*, the booted eagle *Hieraaetus pennatus*, the common buzzard *Buteo buteo*, the northern goshawk *Accipiter gentilis*, the red kite *Milvus milvus* and the peregrine falcon *Falco peregrinus*. Predation of monk parakeets by raptors has been recorded in its invaded range (Burger and Gochfeld 2009; Reed et al. 2014; Briceño et al. 2019), as well in our study area, such as peregrine falcon (Sánchez-Mateos and Sánchez-Albarrán 2017) and golden eagle *Aquila chrysaetos* (E. Navarro pers. comm.). We recorded remains of monk parakeets in several nests of black kites, booted eagles and peregrine falcons and observed their hunting attempts on flying parakeets. The other two raptor species are of similar size and behaviour, and also include birds in their diets (Forsman 1999). Thus, we considered the five raptor species as potential predators. We did not find evidence for other bird species, such as corvids, preying upon monk parakeets or their nests.

For storks and raptors, each nest corresponds to a single breeding pair, whereas for parakeets each nest can house from one to several breeding pairs accommodated in different chambers (range: 1–35 active chambers). A parakeet nest was classified as being associated with a stork if they shared the same nesting substrate, if the parakeet nest was located on the same structure (i.e., the same tree or electricity pylon) as the stork nest, or if the parakeet nest was within a radius of 15 m of a stork nest (Fig.

(Fig.1).1). Although mammals and snakes can predate on parakeets, they were not considered in this study as we do not have accurate information about their distribution and abundance. However, their potential impact on parakeets is discussed based on nest substrate (see previous).

Interactions between parakeets and raptors

We recorded the responses of parakeets towards intruding raptors (i.e., raptors flying within less than 15 m of an active parakeet nest) across the study area, following previous work conducted on a similar species, the rose-ringed parakeet (*Psittacula krameri*; Hernández-Brito et al. 2014). Parakeet responses were classified as stay (i.e., when parakeets stayed in their nests, showing no sign of fear toward the raptor), mobbing (i.e., when parakeets flew to attack the approaching raptor), or flush (i.e., when parakeets flew away from the raptor).

Statistical analyses

We used Generalised Linear Models to test if parakeet-stork associations were more likely in rural than in urban areas (logistic link functions, binomial error distributions) by considering all parakeet nests present in the study area and including the habitat where they were located (i.e., urban or rural) as an explanatory variable. We then evaluated if parakeets used rural stork nests (probability of parakeet-stork association considering all stork nests present in the rural areas; logistic link functions, binomial error distributions) based on a combination of conspecific density, type of substrate and predation risk. Conspecific density was obtained as the relative position of each parakeet nest within the parakeet population. We used the formula $\Sigma exp(-dij)*A$, where dij is the linear distance between each parakeet nest i and all parakeet nests j, and A is the number of chambers per nest j (Moilanen and Hanski 1998). Higher values of this index point to a higher density of conspecifics around a selected location. Predation risk was assessed by using the aggregation of raptors nests as a proxy, calculated using the same index explained previously (note that here *A* always equals 1). Models for the probability of parakeet-stork associations were separately run for 2014 and 2015 because of convergence problems when using generalised linear mixed models and nest as a random term. Finally, we related the probability of nest abandonment by rural parakeets with nest abandonment by the stork (independent variable), considering if colonies occupied in 2014 remained occupied in 2015 (logistic link functions, binomial error distributions). All continuous variables were included in their linear and quadratic forms and standardised before modelling. Model selection was performed using the Akaike Information Criterion corrected for small sample sizes, AICc; (Burnham and Anderson 2002). Within each set of models (which includes the null model), we calculated the ΔAIC*ci* (as the difference between the AICc of model i and that of the best model) and the weight (w) of each model. Models within 2 AICc units of the best one were considered as alternatives and used to perform model averaging (MuMIn package). We considered that a given effect received no, weak or strong statistical support when the 95% confidence interval (CI) strongly overlapped with zero, barely overlapped with zero, or did not overlap with zero, respectively. Statistical analyses were conducted in R 3.1.2 (R Core Team, 2013).

Differences in behavioural responses of parakeets toward approaching raptors were compared among habitats (urban or rural) and between nests associated or not associated with storks using generalised linear models (multinomial error distribution). We included the number of parakeets present in each raptor intrusion and the interacting raptor species as covariates to control for their potential effects.

RESULTS

Protective nest associations

We recorded more than 900 monk parakeet nests, most of them located in the urban habitat, while avian predators were much more abundant in rural habitats (Fig. 2; Table 1). Parakeets nesting in rural habitats were rare and mainly associated with storks (97.06% of parakeet nests associated with storks in 2014, n = 34; 73.53% of parakeet nests associated with storks in 2015, n = 34), an association that was near completely absent among urban parakeets (habitat (urban): estimate: -2.30; 95% CI: − 2.88 - -1.73). Importantly, parakeets bred mainly associated with stork nests located in pylons (70 and 100% of associated nests in 2014 and 2015 were in pylons, Table Table1).1). However, models run for 2014 and 2015 show that the probability of parakeet-stork association was only related to habitat (i.e., more likely in rural than in urban areas; Table 2).

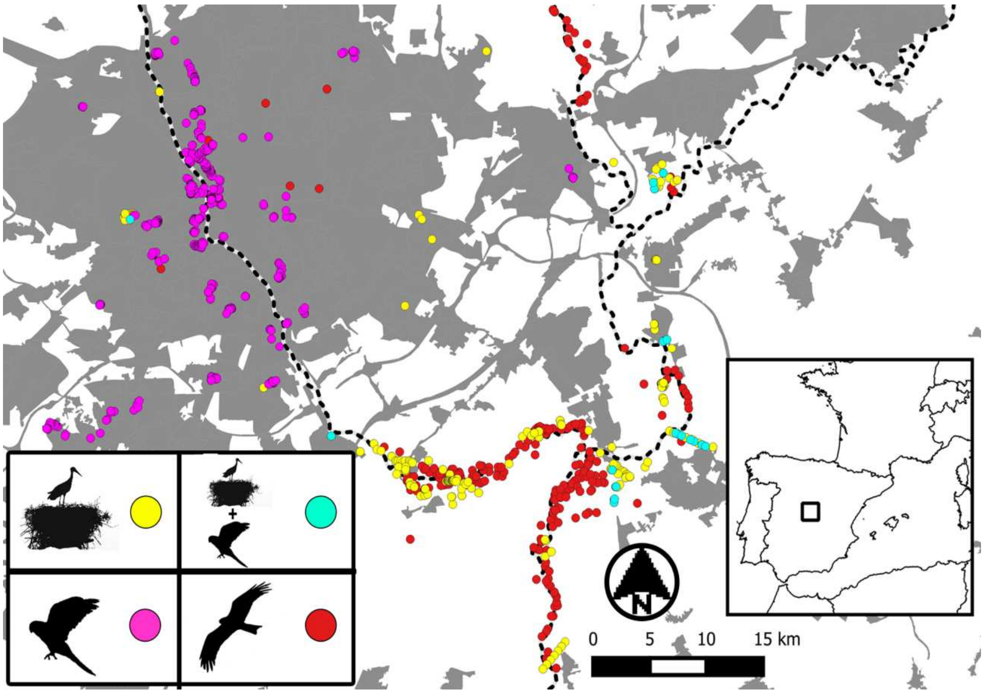

Fig. 2 Study area. Urban (dark grey) and surrounding rural (white) areas of Madrid Metropolitan area (40° 21′ 03.1“ N, 3° 30’ 06.1” W). Different coloured points show the location of nests of raptors (red), storks (yellow), and parakeets associated (blue) or not associated (purple) with storks. Black dashed lines are rivers

Table 1 Abundance of species in the study area. Number of nests of Monk parakeets, white storks and avian predators in urban and rural areas. The type of substrate (i.e., pylon, tree or roof) is indicated for Monk parakeet and white stork nests

Species	**2014**		**2015**	
	Urban	**Rural**	**Urban**	**Rural**
Monk parakeets *Myiopsitta monachus*	867	34	890	34
Associated with storks				
Pylons	0	23	0	25
Trees	9	10	9	0
Roofs	0	0	0	0
Not associated with storks				
Pylons	2	0	2	0
Trees	856	1	879	9
Roofs	0	0	0	0
White storks *Ciconia ciconia*	41	466	47	440
Pylons	6	233	7	209
Trees	32	217	37	216
Roofs	3	16	3	15
Black kites *Milvus migrans*	0	239	0	244
Common buzzards *Buteo buteo*	0	15	0	14
Booted eagles *Hieraaetus pennatus*	0	5	0	4
Northern goshawks *Accipiter gentilis*	0	3	0	3
Red kites *Milvus milvus*	0	1	0	1
Peregrine falcon *Falco peregrinus*	6	0	6	0

Within rural habitats, stork nests were not used at random, and parakeets selected, among those available, stork nests located in areas where conspecifics were more abundant and predation risk was lower (Table 3; Fig. 3). It is worth noting that the correlation between conspecific density and predation risk increased from 2014 to 2015 (− 0.38 and − 0.48, respectively), so predation risk received weaker support in models obtained for the second year. However, when conspecific density was excluded from models, predation risk was strongly related to stork nests also used in 2015 (estimate: -1.34, 95% CI: − 2.60 - -0.47).

Table 2 Factors affecting the probability of association between parakeets and storks. Relative importance of habitat (urban and rural) and type of substrate (pylon, tree or roof) on the probability of protective nesting associations between monk parakeets Myiopsitta monachus and white storks Ciconia ciconia. Estimates and 95% confidence intervals (2.5 and 97.5%) were assessed after model averaging (ΔAIC ≤2). We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero (*), or did not overlap zero (**), respectively. *k*: number of parameters. AICc: Akaike Information Criterion corrected for small sample sizes. ΔAICc: difference between the AICc of model *i* and that of the best-supported model (i.e. the model with the lowest AICc); w: Akaike weights. R^2: measure of how well the model explains the data

Model	**k**	**AICc**	**ΔAICc**	**Weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**	
substrate*habitat + year	5	234.58	0	0.58	substrate (pylon)	18.66	-1814.86	1852.17	
substrate*habitat	4	236.4	1.81	0.24	habitat (urban)	-4.59	-5.61	-3.58	**
substrate + habitat + year	4	237.66	3.08	0.13	year (2015)	-0.85	-1.73	0.03	*
substrate + habitat	3	239.22	4.64	0.06	habitat (urban)*substrate (pylon)	-32.65	-6642.7	6577.41	
habitat*year	4	257.07	22.49	0					
habitat + year	3	260.93	26.35	0					
habitat	2	261.53	26.95	0					
substrate + year	3	318.7	84.12	0					
substrate	2	320.07	85.48	0					
null	1	633.94	399.36	0					
year	2	634.84	400.26	0					

R^2=0.70

Table 3 Factors affecting the probability of association between parakeets and storks in rural areas. Relative importance of predation risk, conspecific aggregation and substrate on the probability of protective nesting associations between Monk parakeets *Myiopsitta monachus* and white storks *Ciconia ciconia*. Estimates and 95% confidence intervals (2.5 and 97.5%) were assessed after model averaging (ΔAIC $\leq$2). We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero (*), or did not overlap zero (**), respectively. Models were run separately for 2014 and 2015. k: number of parameters. AICc: Akaike Information Criterion corrected for small sample sizes. ΔAICc: difference between the AICc of model i and that of the best-supported model (i.e. the model with the lowest AICc); w: Akaike weights. R2: measure of how well the model explains the data

Model 2014	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.50%**	**97.50%**	
predation risk + conspecific density	3	107.56	0	0.67	predation risk	-3.7	-5.47	-1.94	**
predation risk + conspecific density + substrate	5	108.94	1.38	0.33	conspecific density	2.69	1.56	3.81	**
conspecific density + substrate	4	128.75	21.19	0	substrate (pylon)	15.22	-2533.35	2563.8	
conspecific density	2	133.87	26.31	0		16.21	-2532.36	2564.79	
predation risk + substrate	4	173.9	66.34	0	substrate (tree)				
predation risk	2	180.08	72.52	0					
substrate	3	183.32	75.76	0					
null	1	202.61	95.04	0					
Model 2015	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.50%**	**97.50%**	
conspecific density + substrate	4	101.07	0	0.36	conspecific density	2.02	1.19	2.84	**
conspecific density	2	101.39	0.32	0.31	substrate (pylon)	18.4	-13219.31	13256.1	
predation risk + conspecific density	3	102.34	1.26	0.19	substrate (tree)	1.63	-13742.57	13745.84	
predation risk + conspecific density + substrate	5	102.87	1.8	0.15		-0.75	-2.75	1.25	
predation risk + substrate	4	149.78	48.71	0	predation risk				
substrate	3	159.11	58.04	0					
predation risk	2	164.26	63.18	0					
null	1	193.96	92.88	0					

2014: R^2=0.39

2015: R^2=0.40

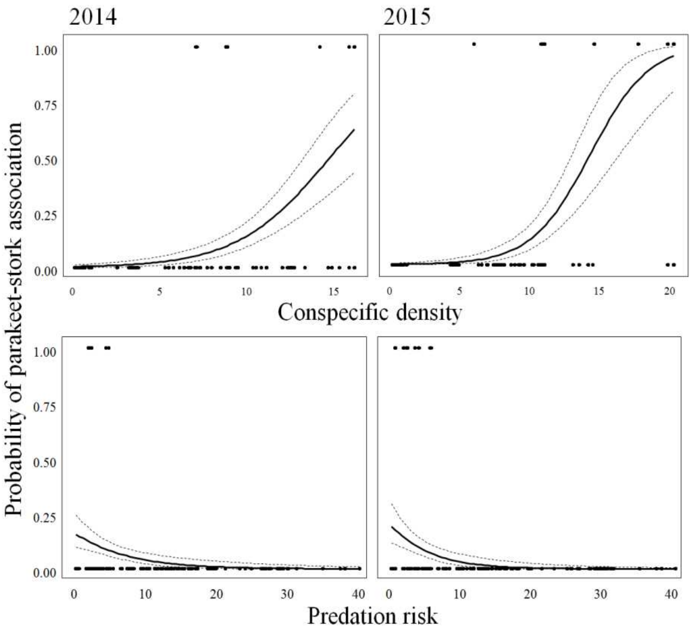

Fig. 3 Probability of parakeet-stork association in rural habitats. Parakeets select rural stork nests located farther from predators (aggregation of predators) and surrounded by larger densities of conspecifics (aggregation of parakeets). Estimates (solid lines), confidence intervals (dashed lines) and raw data (black dots) are shown for 2014 and 2015

Probability of nest abandonment by parakeets

From 2014 to 2015, 44% of the 34 rural parakeet nests were abandoned, while all urban parakeet nests remained active. This high rate of abandonment recorded among rural nests was strongly explained by the abandonment of the nest by the stork (Table 4). Substrate, conspecific density and predation risk were weakly supported, with nests located in pylons, far from conspecifics and in areas with a low density of predators being more prone to abandonment when they were abandoned by storks.

Table 4 Factors affecting the probability of nest abandonment by parakeets between 2014 and 2015. Estimates and 95% confidence intervals (2.5 and 97.5%) were assessed after model averaging (ΔAIC ≤2). We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero (*), or did not overlap zero (**), respectively. Models were run separately for 2014 and 2015. k: number of parameters. AICc: Akaike Information Criterion corrected for small sample sizes. ΔAICc: difference between the AICc of model i and that of the best-supported model (i.e. the model with the lowest AICc); w: Akaike weights. R^2: measure of how well the model explains the data

Model	k	AICc	ΔAICc	weight	Variables	Estimate	2.50%	97.50%	
abandon stork + conspecific density	3	31.88	0	0.37	abandon stork	3.83	0.82	6.85	**
abandon stork	2	32.95	1.07	0.22	conspecific density	-1.03	-2.31	0.25	*
abandon stork + substrate	3	33.01	1.13	0.21	substrate (pylon)	1.81	-0.81	4.43	*
abandon stork + predation risk	3	33.23	1.35	0.19		-0.87	-2.2	0.47	*
predation risk + conspecific density	3	41.39	9.52	0	predation risk				
Null	1	41.42	9.55	0					
conspecific density + substrate	3	42.19	10.32	0					
Substrate	2	42.89	11.02	0					
predation risk	2	42.95	11.08	0					
conspecific density	2	42.96	11.08	0					
predation risk + conspecific density + substrate	4	43.43	11.56	0					
predation risk + substrate	3	45.27	13.39	0					

R2=0.45

Interactions between monk parakeets and predators

We recorded 47 instances in which three different raptor species (the black kite, the booted eagle, and the common buzzard) closely approached parakeet nests, most of them in rural habitats (66%). The number of parakeets present during these intrusions ranged between 1 and 50 (median = 8.7). Parakeets usually flew when raptors approached (57.4%), although in 36.2% of the cases they stayed in the nests. Parakeets attacked the intruding raptor (mobbing) only in three cases (6.4%), all of them in rural nests associated with stork nests. Given the low number of mobbing events, we considered the proportion of flushing events against mobbing and staying (pooled together) between habitats. Parakeets from urban nests flushed in 100% of the raptor intrusions while rural ones only flushed in 31.5% of the events (Fig. 4). This behavioural difference is statistically significant ($\chi^2 = 878.28$, df = 2, $p < 0.001$), even when controlling for the potential effects of the raptor species ($\chi2 = 2.29$, df = 2, $p = 0.318$) and the number of parakeets involved ($\chi^2 = 1.70$, df = 1, $p = 0.192$). Interestingly, within the rural parakeet population, individuals in nests not associated with storks behaved similarly to urban ones (i.e, they flushed in 100% of the raptor intrusions), while parakeets associated with white storks only flushed in 4.8% of the instances (Fig. 4). Again, this behavioural difference is statistically significant ($\chi^2 = 47.56$, df = 2, $p < 0.001$), even when controlling for the potential effects of the raptor species ($\chi^2 = 2.21$, df = 2, $p = 0.331$) and the number of parakeets involved ($\chi^2 = 2.98$, df = 1, $p = 0.084$).

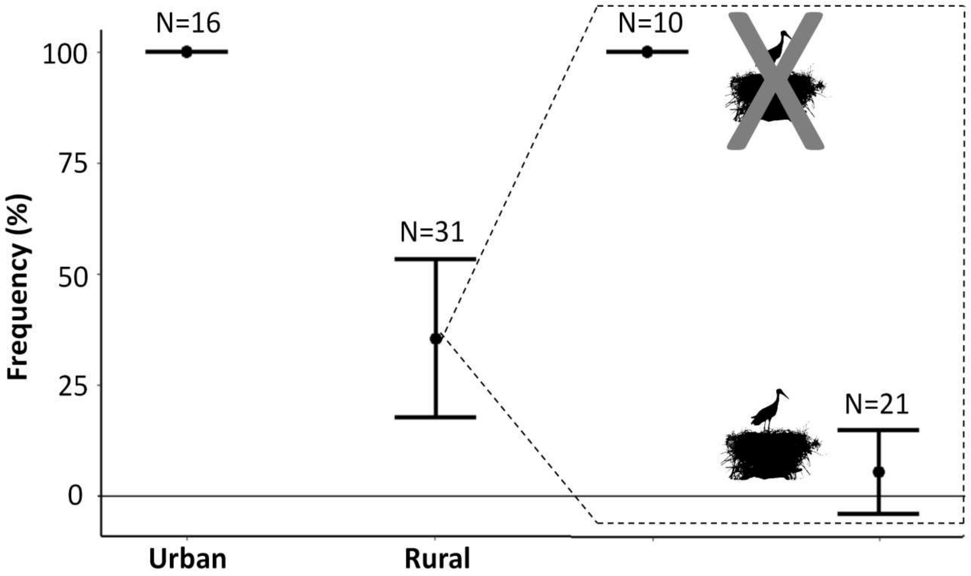

Fig. 4 Antipredatory response of monk parakeets. Frequency of observations (mean and 95% CI) in which nesting monk parakeets flushed when approached by a predator (raptor) in urban and rural habitats. For rural individuals, the frequency of birds flushing is separately shown for nests associated or not associated with storks

DISCUSSION

Most hypotheses dealing with biological invasions focus on factors that increase invasion success while very few focus on aspects that inhibit them (Catford et al. 2009). Among the later, studies about interactions between invasive species and their recipient communities have long focused on biotic resistance, mainly through competition and predation (Braga et al. 2018). However, some positive interactions with native species may also arise and assist invasive species in establishing populations in novel areas, increasing their potential niche and thus, invasive potential (Bruno et al. 2003). In this way, recent studies have shown the important role played by mutualisms in enhancing invasions of many exotic plants and invertebrates (Traveset and Richardson 2014). However, to our knowledge, there is no published information on protective associations favouring vertebrate invasions. Here, we show how nesting in association with a protective, much larger native species may favour the colonisation of natural habitats by a species typically restricted to urban areas in its invasive range, the monk parakeet. This example, representing another form of ecological facilitation, namely commensalism (i.e., a species interaction in which one species benefits and the other is unaffected), has been more rarely documented (Rodriguez 2006) and can also be important in assisting invasive species.

Nesting associations between monk parakeets and other stork species have been previously described in South America (the native range of parakeets). However, the authors argued that the main benefit of these assemblages is related to structural safety, noting its potential antipredatory role as a secondary advantage (Burger and Gochfeld 2005). In our study area, results suggest that the principal explanation for parakeet-stork associations is the deterrence of predators, not the facilitation of nest building. First, records of nesting associations with storks are rare in urban areas, which is unexpected if the main reward is structural benefits. Conversely, all nesting associations occurred in rural areas, where predators were much more abundant. Second, the abandonment of a stork nest by parakeets was related to its previous abandonment by storks, in line with expectations if the protective association allows parakeets to colonise otherwise unsuitable areas in terms of predation risk. Third, when comparing the behavioural responses of parakeets toward predators in rural and urban areas, we found that urban birds, which are not associated with storks, always flushed when approached by a predator. The same behaviour was observed among rural parakeets not associated with storks, while almost none of the rural parakeets nesting with storks flushed when a raptor approached their nests. Fourth, contrary to Burger and Gochfeld (2005), we considered as associated nests not only nests sharing the structure of the stork nests but also those located within a close radius of the stork nests, thus without direct structural benefits. We can assert that this nesting association, rather than facilitating nesting substrate, offers antipredatory protection that allows the spread of the invader from urban into rural areas.

Although protective nesting associations with storks may overcome the biotic resistance offered by the rural predator community, the importance of predation risk in the distribution of monk parakeets was evident when we analysed the location of these protective associations within the distribution of rural stork nests. From all stork nests available, parakeets tended to associate with those located farther away from predators and surrounded by larger densities of conspecifics. Although storks provide a protective umbrella to parakeets, this protection is restricted to the nearby surroundings of the nest site (Quinn and Ueta 2008). Thus, breeding farther from predators may allow parakeets to perform their daily activities such as foraging in areas with lower predation risk. Accordingly, the importance of breeding close to conspecifics can also be explained in terms of reducing predation risk (Wittenberger and Hunt 1985; Navarro et al. 1992; Brown and Brown 2001), through both cooperative defence and dilution effects (Wrona and Dixon 1991; Bednekoff and Lima 1998; Beauchamp 2014).

Non-native species tend to proliferate more frequently in human-altered habitats compared to less altered ones (Sax and Brown 2000). Some bird species such as parrots fit well to this pattern, as they are not only more frequent and abundant in such environments, mainly urbanised ones (Cardador et al. 2016; Abellán et al. 2017), but because many of them seem to be unable to expand to more pristine habitats despite their well-developed flying abilities (Case 1996; Sol et al. 1997). Although the reasons are unclear, some authors have proposed that the higher biotic resistance often recorded in more natural communities can preclude the colonisation of more natural habitats by exotic species (Diamond and Veitch 1981; Evans et al. 2009; Sol et al. 2014). In this sense, predators can exert strong top-down regulative processes on prey populations, mainly when populations are small (Newton 1998) as occurs during the first stages of the invasion process, when populations of invasive species are still incipient and, thus, particularly vulnerable to predation (Cassey et al. 2005). For monk parakeets, predation of eggs, chicks and adults in the nests is the most common cause of breeding failure and mortality during the breeding season (Martella and Bucher 1984; Martella 1985; Navaro et al. 1992; Eberhard 1998). Thus, although the species expanded into the rural habitats of the study area in the 1990s (four breeding colonies) when the predator community was much less abundant (Blanco 1994), they failed to successfully establish likely due to the progressive recovery of the predator community since the early 2000s onward (G. Blanco and Ó. Frías, unpubl. data). Spanò and Truffi (1986) also recorded the extinction of an emergent monk parakeet population in Italy in 1948 due to constant nest predation by rats, supporting the role of predation in the establishment success of this invasive species.

The management of invasive species in cities is controversial, mainly when the best management option, from an ecological perspective, is the eradication of charismatic species. Ethical conflicts are particularly exacerbated when these species are aesthetically appealing mammals or birds that have become the most visible, non-domesticated animals present in public areas (Bertolino 2009). In those cases, for social and pragmatic reasons, some authors have suggested that these species should be accepted as part of the urban ecosystem if their risk of spreading toward natural areas is reduced (Gaertner et al. 2016). However, the limited capacity of some non-native species to spread from urban habitats may only represent a transient stage related to lag phases, which are expected when evolutionary change -including the evolution of invasive life-history characteristics, the purging of genetic load responsible for inbreeding depression or the evolution of adaptations to the new habitat- is an important part of the colonisation process (Sakai et al. 2001; Crooks 2005; Lockwood 2013). Spread lag phases may take years or decades, can vary among species and populations of the same species subject to different ecological conditions (Aagaard 2014) and are highly unpredictable (Coutts et al. 2018). Therefore, it is not prudent to assume that exotic species that have been observed in urban areas for a long period will remain strictly urban in the future. In fact, the distribution of monk parakeets invading Israel has increased and shifted from predominantly urban areas to agricultural landscapes in less than two decades (Coutts et al. 2018). This may have been facilitated by the long-term decline and poor conservation status of raptors in that country (Yom-Tov et al. 2012). Thus, accepting invasive species as part of the urban ecosystem may sometimes result in their spread into adjacent rural landscapes, where they could have different, often unknown impacts (Botham et al. 2009, Moreira-Arce et al. 2014), such as crop damage in the case of monk parakeets (Senar et al. 2016; Postigo et al. 2017).

The monk parakeet was first introduced in Spain in 1976, increasing its distribution since then at a rate of 8.14 grid cells (5 × 5 km) per year (Abellán et al. 2017). However, it was not until recently that the Spanish population began to grow exponentially, increasing from c. 6000 individuals in 2010 to c. 20,000 in 2015 distributed across > 130 urban populations (Molina et al. 2016). Therefore, it seems that the species has overcome the lag phase, and the protective nesting association facilitating its spread outside of cities, rather than anecdotal, may be occurring in other areas. Predictive models indicate that there is still plenty of suitable habitat for the species (Muñoz et al. 2006; Molina et al. 2016). Furthermore, white storks are widely distributed across Spain (with > 33,000 nests in 2004; Molina et al. 2004) and populations are rapidly increasing thanks to the use of human-related food subsidies (invasive American crayfish and rubbish dumps (Blanco 1996; Tablado et al. 2010; Sanz-Aguilar et al. 2015). In fact, in recent years, monk parakeets also spread from another Spanish city (Zaragoza, 270 km distant to Madrid), by nesting in stork nests (J.L. Tella obs. Pers.), but such a spread was halted by the responsible authorities by shooting the whole parakeet population. Therefore, the risk of monk parakeet expansion from urban habitats, thanks to the widespread distribution of white storks, should be considered when designing management strategies for this highly invasive species, which is growing exponentially in Mediterranean countries (Postigo et al. 2019), including Spain, Portugal, France, Italy, Greece, Morocco, and Israel, where the two species coexist (Hagemeijer and Blair 1997; Postigo et al. 2019). Management actions could be required in the case rural populations of monk parakeets would cause significant impacts (Postigo et al. 2019), although these actions usually show low support from the society (Shackleton et al. 2019), even lower when dealing with charismatic species such as parakeets (Crowley et al. 2019). Consequently, more research and awareness campaigns are necessary not only to know the actual magnitude of the impacts derived from invasive species (Blackburn et al. 2010) but also to make management actions effective. In our case, actions only focus on the avoidance of monk parakeets nesting in white stork nests may not be efficient. On the one hand, anti-nesting devices installed in pylons for white storks do not prevent their nesting, even after great management efforts (Maricato et al. 2016). On the other hand, nest removal would be not efficient because both species show strong fidelity to their nesting substrates and often rebuild their nests very soon (Sol et al. 1997; Vergara et al. 2006; Pruett-Jones et al. 2007; Burger and Gochfeld 2009). Contrarily, actions aimed to improve predator populations as biological controllers, should be effective to halt the spread of this species into rural areas in the long term.

This study assesses the nesting association between an invasive bird, the monk parakeet, and a native bird species, the white stork, showing a commensalism relationship in which parakeet colonies associated with stork nests benefit from the effective antipredatory defence of storks. This association was more likely in rural areas, where predation pressure is higher than in nearby urban ones, assisting thus the spread of monk parakeets across the rural environment. Moreover, the abandonment of parakeet colonies after the previous nest abandonment of associated storks, as well as their different behavioural reactions against raptors when associated with storks, suggest that parakeets have a strong dependence of their hosts. However, this protective association is limited as parakeet colonies also avoided high densities of breeding raptors in the study area. Without the facilitation provided by storks, the biotic resistance from the raptor community prevents the invasion success of parakeets. Future studies are needed to assess the complexity of interactions between invasive species and the recipient community, which may be fundamental to develop effective management plans against biological invasions.

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SECTION 3:

ANIMAL-PLANT INTERACTIONS

Chapter VIII

The extent, frequency and ecological functions of food wasting by parrots

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ABSTRACT

Anecdotic citations of food wasting have been described for parrots, but we lack a comprehensive knowledge about the extent of this behaviour, and its ecological and evolutionary implications. Here, we combine experimental and observational approaches to evaluate the spatial, temporal, typological and taxonomic extent of food wasting by parrots, to identify the ecological and evolutionary factors driving food wasting, and to assess the incidence of two ecological functions derived from food wasting, such as food facilitation to other animal species and secondary seed dispersal. We found that food wasting is a widespread behaviour found in all the studied parrot species. However, the proportion of food wasted differed among species and throughout the year. Parrots wasted more food during the non-breeding season, when they relied on exotic plants and on unripe fruits or seeds. We also recorded 86 animal species feeding on the food wasted by parrots, 27 of which potentially acted as secondary seed dispersers. Overall, our study emphasizes the universality of food wasting among parrots, and the important implications that this behaviour may have for the species involved (i.e., the parrot, the plant, the other species feeding on wasted food), and for the functioning of the whole ecosystem.

INTRODUCTION

The way species interact with each other may have overarching implications for community organization and ecosystem functioning (Bascompte and Jordano 2007; Bastolla et al. 2009; Sebastián-González et al. 2011). For example, several studies have documented that mutualistic animal-plant interactions, such as seed dispersal or pollination, drive important coevolutionary forces shaping the structure of both animal and plant communities (Guimarães et al. 2011; 2017). Likewise, animal species may use each other as indicators of habitat quality, affecting the final distribution of the species in the communities (Sebastián-González et al. 2010). Therefore, it is important to identify how species interact with each other and to understand the mechanisms shaping these interactions.

An interesting understudied behaviour related to interacting frugivorous animals and fruit-producing plants is food wasting (hereafter, waste). Howe (1980) found that monkeys discarded almost two-thirds of the seeds they handled, while Bosch & Wedde (Bosch and Wedde 1981) described how some parrots ate fruits only partially, discarding the rest. Anecdotic citations of waste by parrots can also be found in other dietary studies, both in places where animal species are native (Galetti and Rodrigues 1992; Galetti 1993; Symes and Perrin 2003; Blanco et al. 2018) or exotic (Masrtens et al. 2013). However, we lack a comprehensive understanding the ecological and evolutionary implications of this behaviour, as well as its implications.

Food wasting is illogical under classical ecological theories of resource use, where optimal foragers move between alternative patches (Chamov 1976) or diet items (e.g.; Tinker et al. 2008) to prevent the total depletion of a particular resource. Predators may also maintain prey consumption within sustainable limits to ensure the viability of prey species (Slobodkin 1968). Then, why do animals waste food? Some authors propose that waste may be an accidental behaviour. Frugivorous and granivorous species may unintentionally drop fruits and seeds while handling them during the foraging process (Avery et al. 1993; Rey et al. 1997), larger fruits being involuntarily dropped with a higher frequency than small ones (Avery et al. 1993). Other unexplored factors that may affect accidental dropping are conspecific disturbance or the coevolutionary history of the animal and the plant species. Conspecific density may affect waste, as individuals foraging in larger groups may drop more food than those in small ones. Besides, animals may drop more fruits from exotic than from native plants because they have had shorter evolutionary times together to get used to them. However, frugivores may also deliberately drop low-quality fruits such as those parasitized (Symes and Perrin 2003), unripe, or those with low energetic and nutritional content (Foster 1977). In these cases, if waste is not accidental, individuals may be able to adjust this behaviour according to food availability, as dropping food when it is abundant does not have a large energetic cost.

Despite the uncertainty about why parrots waste food, several studies have suggested that this behaviour may benefit other species (Galetti and Rodrigues 1992; Galetti 1993; Martens et al. 2013). For example, dropped fruits or seeds become available to ground dwelling animals that otherwise cannot benefit from them (Galetti and Rodrigues 1992; Galetti 1993; Martens et al. 2013). Besides eating them, these species can also act as secondary dispersers (Galetti and Rodrigues 1992; Galetti 1993; Symes and Perrin 2003; Martens et al. 2013; Blanco et al. 2018), increasing the number of different dispersal modes for the plant involved and, thus, the chances of effective dispersal. However, we do not know to what extent wasted food is consumed or secondarily dispersed by other species (Barnett et al. 2012).

Parrots (Psittaciformes order) are an evolutionarily old and diversified animal group (Tod and Wright 2015) where waste has been anecdotally observed, but never quantified. Therefore, we combined experimental approaches with fieldwork conducted in five continents to understand the importance of this behaviour across parrot species, its drivers and the consequences for other species. Table 1 summarizes the hypothesis tested about waste by parrots, as well as the associated predictions. Briefly, we evaluate the spatial, temporal, typological and taxonomic extent of waste by parrots. If waste is an anecdotal behaviour, we expect to find it only in few parrot species. Otherwise, if waste is a widespread behaviour, we would find it in most parrot species, independently of their evolutionary history and their region of origin.

Table 1 Tested hypotheses, associated predictions, reasoning of the prediction, variable used to test the prediction, dataset used and verification of the prediction based on our

Hypothesis	Prediction	Rationale	Variable	Dataset used	Verified?
Waste is widespread	1. Waste happens in many species, all the year, on many plant parts, in all biogeographic regions		Presence of waste	Field transects	Yes
				Experiment	Yes
	2. Waste is independent of the evolutionary history of the species		Phylogenetic signal	Experiment	Yes
	3. Waste may happen in large amounts		Amount of food wasted	Experiment	Yes
				Waste quantification	Yes
Waste is not random	4. Waste occurrence and quantity differ among species	Species differ in their handling abilities and foraging strategies	Presence of waste	Field transects	Yes
			Amount of food wasted	Experiment	Yes
Waste is accidental	5. Waste is more frequent in large bird groups	Because of conspecific disturbance	Number individuals trial	Experiment	No
	6. Waste is more frequent with exotic plant species	Because parrots are less used to them	Origin plant	Field transects	Partially
Waste is deliberate	7. Amount of food wasted is larger in large species	Small species have fast metabolisms and need to optimize resources	Body mass	Experiment	No
	8. Waste is lower when food availability is reduced	To cover nutritional requirements	Fasting	Experiment	No
	9. Wasted food is less energetic (unripe)	Parrots select high-quality food	Ripening status	Field transects	Partially
	10. Waste is more frequent outside the breeding season	Because energetic requirements are higher during breeding	Season	Field transects	Yes
	11. Wasted food has more parasites	Parrots select high-quality food	Parasites presence	Waste quantification	No
Waste benefits other species	12. Waste is large under the tree	Attracts animals	Num. fruit/seed under tree	Waste under tree	Yes
	13. Wasted food is used by a variety of species	Because it is a good alternative resource	Species detected	Camera traps	Yes
				Direct observations	Yes
	14. A number of benefited species may also act as secondary dispersers, with different dispersal distances		Detected species traits	Camera traps	Yes
				Direct observations	Yes

Then, we assessed if waste is a random process, independent of parrot life traits. To so do, we looked for differences in waste occurrence and amount of food wasted among species to identify the ecological factors driving waste. We hypothesized that this behaviour can be either accidental (i.e. plant parts fall because of difficulties during handling) or deliberate (i.e. parrots decide to waste food). Accidental waste may happen with a higher frequency when individuals forage in large groups, because of conspecifics disturbance, or with exotic plants, because parrots are less used to handle them. Contrarily, if waste is deliberate, this behaviour should happen more frequently with low-quality fruits and seeds (e.g. parasitized and unripe), and when energetic requirements are softer (e.g. outside the reproductive season, or when food availability is high). We also predict that smaller species will waste less food because they have a faster metabolism than large species (e.g.; Lovegrove et al. 2011) and need to optimize food intake. Lastly, we hypothesized that wasted food can benefit other species, so we assessed the extent and incidence of two possible ecological functions derived from waste: food facilitation to other animal species and seed dispersal. If wasted food is beneficial for the plant and for other species, we expect that the number of seeds underneath the trees where parrots have wasted food will be large and will attract many species. We also expect that waste will benefit a large number of different species with different potential dispersal modes. Finally, we discuss some possible ecological functions of waste and their ecological and evolutionary consequences.

MATERIAL AND METHODS

Datasets used

To test our hypotheses about waste, we combined information gathered using different approaches and unified in five different datasets (All of them available as Supplementary Material).

Dataset 1

Experiment in captivity. We first quantified waste experimentally using captive individuals. We performed 362 experimental trials using 130 individuals from 40 parrot species belonging to 24 genera (body weight range: 33–550 g) to measure the proportion of food wasted by the species. Individuals were kept in groups of 1–4 individuals, simulating their typical aggregated foraging behaviour. As cages used for the experiment always have the same size, experiments done including a larger number of individuals simulate situations of higher conspecific disturbance. Parrots were acclimated to the cages and diet for 10 days prior to the experiment. In a third of the experiments, individuals were fasted 24 hours before the start of the experiment, to simulate low food availability. Each species was fed with the typical food used in captivity (e.g. mixtures of millet, birdseed, sunflowers, and peanuts). Food was weighted (±0.1 g) and provided ad libitum to the parrots. Cages were set so that wasted food could not be eaten by individuals after falling to the cage floor. Each group of birds was tested approximately five times, and each trial lasted 24 hours. Wasted food was weighted, including only those seeds that were intact (i.e. half consumed seeds were not included). Finally, we calculated the proportion of food wasted by each group of parrots in each trial. All experimental protocols are in accordance with the relevant guidelines and regulations. Birds were kept in captivity under permit SGYB/FOA/AFR from the Consejería de Medio Ambiente, Junta de Andalucía, in the authorized centre for experimental avian research SE/16/U (REGA ES410910008016).

Dataset 2

Field transects. We collected observations of waste in different fieldwork campaigns performed in 17 countries and 5 continents (Fig. 1a). We looked for groups of foraging parrots in pre-defined roadside and walking transects (see details about transects on47). Every time we detected a foraging group, we observed focal parrot groups or individuals for 5–10 minutes and annotated the occurrence of food wasting (1/0), the parrot species, the plant species consumed, the part of the plant that was wasted (flowers, fruits, seeds, bark, leaves, twigs, sprouts, stems, resin or invertebrates), flock size, the season when the observation was taken (breeding/non-breeding), the ripening stage of the fruits/seeds (unripe/ripe), date, site and the origin of the plant where the observation was taken (native/exotic). This dataset includes a total of 6253 observations of foraging parrots observed between 2011 and 2019 in 37,612 km of transects.

Dataset 3

Waste quantification. We quantified the proportion of food wasted in the field by observing the foraging behaviour of individuals detected handling fruits or seeds during the field transects. For this and the following datasets, and for the statistical analyses in this study, we focused on fruits or seeds and excluded other wasted plant parts because fruits and seeds are the main food types wasted by parrots (see Fig. 1). Foraging individuals were observed from a distance with binoculars or telescopes. We identified the bird and plant species, and we counted the flock size and the number of fruits/seeds each individual ate or wasted. We then calculated the proportion of food wasted as the number of wasted fruits/seeds divided by the total number of fruits/seeds handled. We compiled 412 observations of individual birds from 20 species in Bolivia, Costa Rica, Namibia, Brazil, Peru, Argentina and Spain, between 2014 and 2019. Data was collected during six different months in both the breeding and non-breeding season, and birds handled 1841 fruits and 934 seeds. As some studies suggest that parrots may be wasting parasitized fruits or seeds (e.g.Symes and Perrin 2003), we also counted the total number of wasted fruits with worms for 176 fruits under 7 different tree species during fieldwork in the Brazilian cerrado in 2017.

Dataset 4

Waste under tree. We estimated the number of fruits/seeds a group of parrots could waste per individual tree. To do so, we counted the total number of intact and wholly or partially eaten fruits/seeds under a tree after a group of parrots foraged on it. We also identified the plant species. When the number of fruits was very large or the area was hard to screen because of the dense vegetation, we counted half of the area under the tree and then doubled the number of fruits/seeds. We compiled information on 98 trees from 29 species in Australia, Peru, Ecuador, Bolivia and Brazil between 2013 and 2017.

Dataset 5

Camera traps and direct observations. We used 96 camera traps to monitor the animal species using fruits and seeds wasted by parrots. Cameras were located under the plant, in front of a bunch of fruits/seeds. They stayed activated 5–7 days during 24 hours. Data was gathered in Brazil and Bolivia, under four different plant species where waste had been observed: Attalea totai, A. barreirensis, A. speciosa and Mauritia flexuosa. From the pictures, we separated species that consumed the fruits/seeds and those that took entire fruits/seeds out of the camera, thus being possible secondary seed dispersions. We combined this information with 293 direct observations of food facilitation and secondary dispersal taken in Australia, Spain, Puerto Rico, South Africa, Argentina and Sri Lanka between 2012 and 2019.

Food wasting extent

To test our first prediction (P1) and describe the spatial extent of waste, we identified all the areas around the world where we had observed waste in the wild. The temporal extent of waste was described as the total number of waste events recorded per month. We also calculated the total number of waste events for ring-necked parakeets Psittacula krameri, the species with the largest number of waste events detected. For the temporal extent we used the Field transects dataset, as this is the largest compilation of waste events taken using a standardized method. This same dataset was used to identify the typological extent of waste by counting the total number of waste events found for each plant type (flower, fruit, seed, bark, leaves, twigs, sprouts, stems or invertebrates). Finally, the taxonomic extent of waste by parrots was quantified by identifying the total number of parrot species that was found wasting food and the total number of plant species that were subject to waste by parrots in any of our datasets, and in non-systematic observations performed during fieldwork.

Our second prediction (P2) that waste is independent of the evolutionary history of the species was explored using data from the Experiment. We assessed if there was a phylogenetic signal in the proportion of food experimentally wasted by the different species using the descriptive statistics K (Blomberg et al. 2003). When $K < 1$, the relatives resemble each other less than expected under the Brownian motion evolution, while when $K > 1$ close relatives are more similar than expected under the Brownian evolution. We evaluated the statistical significance of the phylogenetic signal by comparing the observed variance of independent contrasts of the proportion of food experimentally wasted by the different parrot species to a null model of shuffling taxa labels across the tips of the phylogeny. We calculated K and the statistical significance of the phylogenetic signal for 100 bird phylogenies from Jetz et al. (Jetz et al. 2012) using the picante package (Kembel et al. 2010) in R version 3.5.351.

Finally, we evaluated the proportion of food wasted (P3) using two datasets: the Experiment and the Waste quantification. We used the average (±SD) proportion of food wasted by each group of parrots in each trial for the Experiment data and the average (±SD) number of wasted fruits/seeds by each individual parrot for the Waste quantification data.

Waste differences among species

If food wasting is a not a random process (P4) waste occurrence and quantity should differ among species. We used the Field transects data to compare waste occurrence (1/0) among species and the Experiment dataset to compare the proportion of food wasted among species. To test if waste occurrence differed between species, we fitted a Generalized Linear Model (GLM) in R with species as a predictor variable and occurrence as a response variable, using a binomial distribution. We then compared the proportion of food wasted (response variable) among species (predictor variable) in the experiment by means of Generalized Linear Mixed Models (GLMM) using a beta distribution with the glmmADMB library (R Core Team 2019). Because the same individuals were used for different trials, we included individual (or group of individuals) as a random factor in all the models. In both cases, we compared the model including species as predictor variable with a null one. Models with a difference in AIC smaller than 10 were considered equally supported.

Factors driving food wasting

Waste may be driven by different factors, depending on its accidental or deliberate behaviour (predictions 5–11, Table 1). Because the different factors affecting waste may be related, we fitted multivariate models including several predictor variables at the same time. We ran one model for waste occurrence (1/0) (Field transects dataset) and one for the proportion of wasted food (Experiment dataset). Experiment data were used to relate the number of individuals in the cage during the trial (P5), parrot body size (mean weight in g, P7) and the reduction in food availability (simulated by a fasting period, P8) (predictor variables) with the proportion of food wasted (dependent variable) by means of GLMMs using a beta distribution. We included individual (or group of individuals) as a random factor in all the models, nested within species. The weight of the birds was standardized before modelling (i.e. transformed to have a mean of 0 and standard deviation of 1).

Then, we evaluated factors affecting waste occurrence (1/0) in relation with the season when the observation was taken (breeding/non-breeding, P10), the ripening stage of the fruit/seed (unripe/ripe, P9) and the origin of the plant where the observation was taken (native/exotic, P6). We also included the number of individuals in the flock as a covariate in the models to control for the potential effect of larger flocks having a higher chance of showing waste. To test the consistency of the results, we performed the analyses for all the species, but also for the species with the largest number of observations (*P. krameri*); additionally, only for *P. krameri* in the study site with a larger number of observations (Seville, Spain, where the species is introduced) and finally, for all species excluding P. krameri. We fitted Generalized Linear Models (GLM) in R using a binomial error distribution for the models for *P. krameri* and

GLMMs with species as a random term for the model with all the species and for the model with all the species, but excluding *P. krameri*.

As some studies suggest that parrots may be wasting parasitized fruits or seeds (P11), we calculated the proportion of wasted fruits or seeds that were parasitized for 176 fruits found underneath seven different tree species.

Ecological functions of food wasting

To test if waste is large under the tree (P12), we used the Waste under tree dataset. We calculated the mean (±SD) number of intact and partially eaten fruits/seeds under a tree. We also identified the maximum number of intact and partially eaten fruits and seeds found.

We finally evaluated two possible ecological functions of waste by parrots, facilitation of food to other species and secondary seed dispersal (P13 & P14), using the Camera traps and direct observations dataset. For each species benefiting from wasted food, we identified its taxonomic group (i.e. ant, bird, mammal, reptile or fish) and estimated its body size (i.e. very large [>10 kg], large [>1 kg], medium [>0.1 kg], small [>0.01 kg], very small [<= 0.01 kg]) using published studies (see reference list in Dataset). For those species detected acting as secondary dispersers, we also identified the mean dispersal distance from the literature (i.e. very large [>100 m], large [>30 m], medium [>10 m], small [<= 10 m]).

RESULTS

Food wasting extent and randomness

Waste by parrots is a widespread behaviour in many aspects (P1, Fig. 1). It was found in all the study sites visited (35 biomes, 17 countries and 5 continents), in native and introduced parrot ranges. Waste was observed throughout the year, in both the breeding and non-breeding season. Parrots wasted mainly fruits and seeds, but also flowers, leaves, twigs, stems, sprouts, parasites and bark. We observed 103 parrot species (40 species in the experimental approach, 75 in the field and 12 in both the experiment and the field) from 38 genera wasting food from 336 plant species belonging to 80 families (see Supplementary Tables S1 and S2 for complete lists of parrots wasting food and plants where waste occurred).

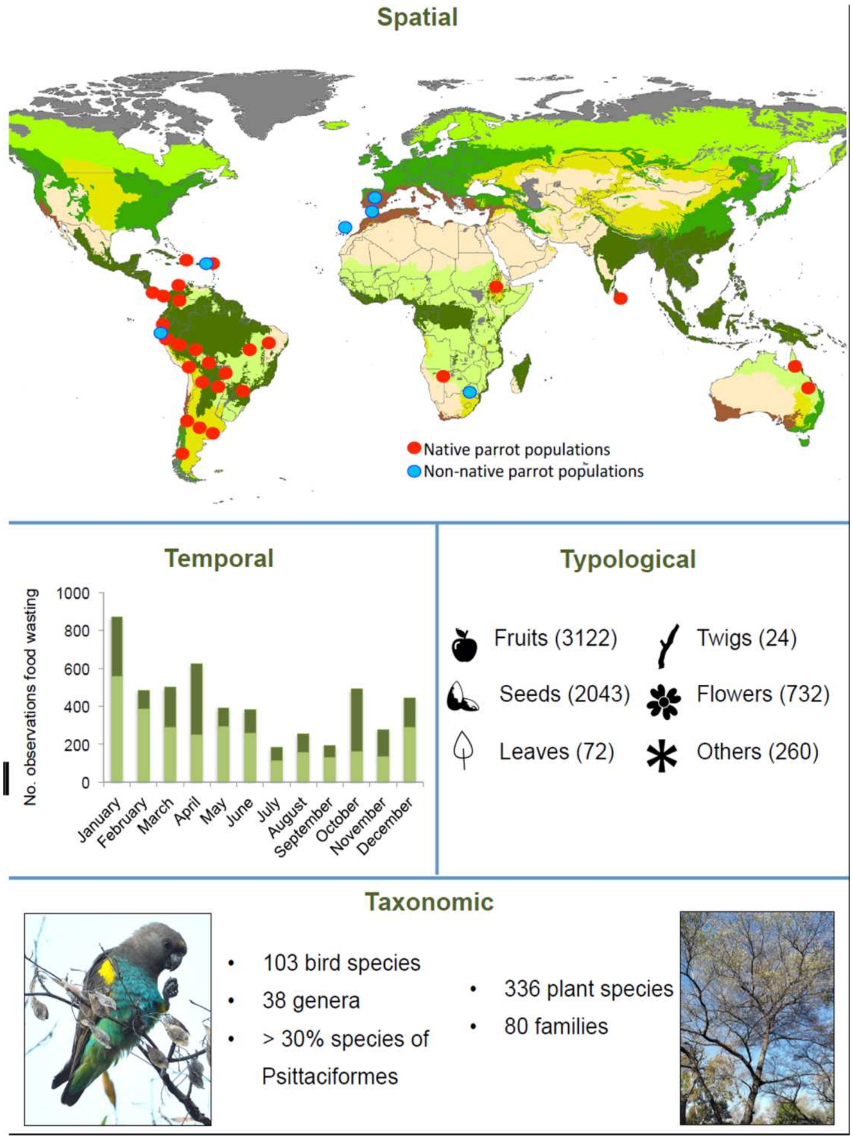

Figure 1. The spatial, temporal, typological and taxonomic extent of food wasting by parrots: Spatial: Each circle shows a surveyed area. Blue circles represent areas where parrots are exotic species, while red circles are areas included in their native distribution. Temporal: The graph shows the total number of waste observations per month by all parrot species (light green) and, specifically, by *Psittacula kramerii* (dark green). Typological: Number of observations for different plant parts wasted by parrots. Others include invertebrates, stems, sprouts, resin and tree bark. Taxonomic: Number of bird species found wasting food and plant species involved. Pictures: Poicephalus meyerii (left) wasting Terminalia sericea fruits and seeds (right), pictures by J.L. Tella. Icons authors: Georgiana Ionescu (fruit), Shawn Erdely (seed), Mansion@design (flower), Noël Rasendrason (twig), Myly (leave) and Lisa Staudinger (asterisk), all from thenounproject.com.

Following our expectations (P2), waste was independent of the evolutionary history of the species, as it did not show a significant phylogenetic signal using any of the 100 phylogenies used (mean K: 0.104, range: 0.007–0.165, all $P > 0.409$). Besides, we found that the percentage of waste by parrots was large (P3), as it averaged 21.2% (SD = 13.0) of the total food provided to individuals during an *in-captivity* experiment (range: 0.4–72.7%). In the wild, we found that parrots wasted 11.8% (SD = 25.1) of the fruits and 14.6% (SD = 20.3) of the seeds that they handled, ranging from lack of waste to a waste of all the fruits or up to 80% of the seeds.

Moreover, we found strong among-species differences in waste occurrence in the wild (δAIC with null model 2882) and in the proportion of food wasted during the experiment (δAIC with null model 12, Fig. 2), suggesting that food wasting is not a random process (P4).

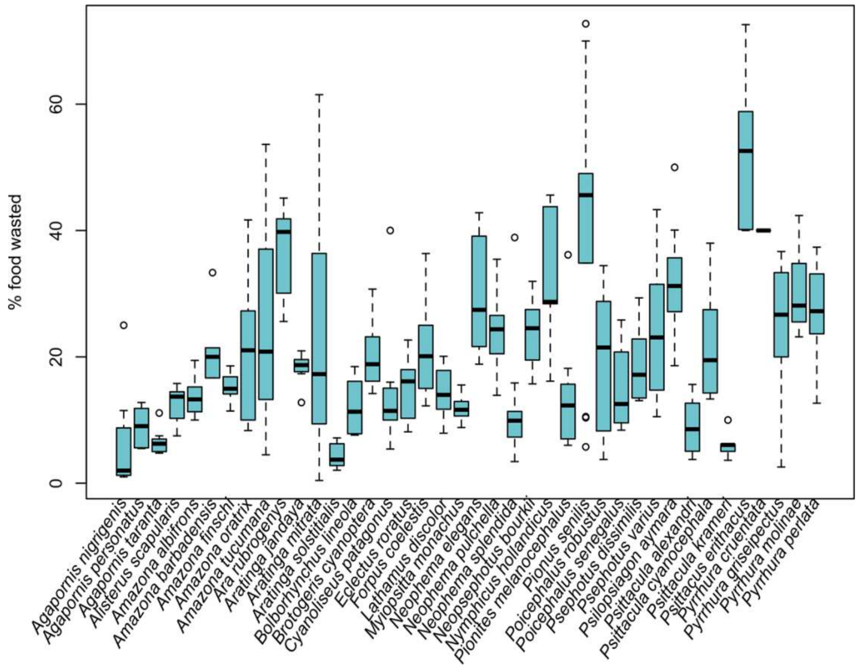

Figure 2. Boxplot of the percentage of food wasted by the 40 parrot species included in the experiment.

Factors driving food wasting

Using a large database of field observations about waste occurrence we identified some factors affecting the occurrence of this behaviour. Fruit and seed wasting were more frequent during the non-breeding season (P10), in exotic plant species (P6) and on unripe fruits or seeds (P9) for all the species. We also repeated the analyses considering only data from *P. krameri*, which is the parrot species with more detailed information, and we observed the same pattern, both including all observations collected across the world and only those observed in Seville, the population with more information (Table 2, Fig. 3). This last analysis corroborates results obtained using the whole data. However, the analyses for all species but excluding *P. krameri* indicate that the season was the only factor driving waste occurrence.

Table 2. Models relating food wasting frequency (1/0) in foraging flocks with the number of individuals in the foraging flock (flock size), the season when the observation was taken (breeding/non-breeding), the ripening stage of the fruit/seed (green/ripe) and the origin of the plant (native/exotic) where the observation was made.

	All species	***P. krameri***	***P. krameri* (S)**	**Excluding *P. krameri***
N	4716	3141	1278	1575
Intercept	1.898	1.125	–0.593	2.398
Log (flock size)	0.358***	0.424***	0.703***	0.207*
Season: Breeding	–0.384***	–0.369***	–0.949***	–0.392*
Status: Green	0.455***	0.599***	0.820***	0.149
Plant: native	–0.298**	–0.372**	–0.983***	–0.199

The model for all species and for all species except *P. krameri* included the bird species as a random term. We show the number of observations used in each model (N), the coefcients of each variable. P-values as follows: ***P<0.001, **P<0.01, *P<0.05

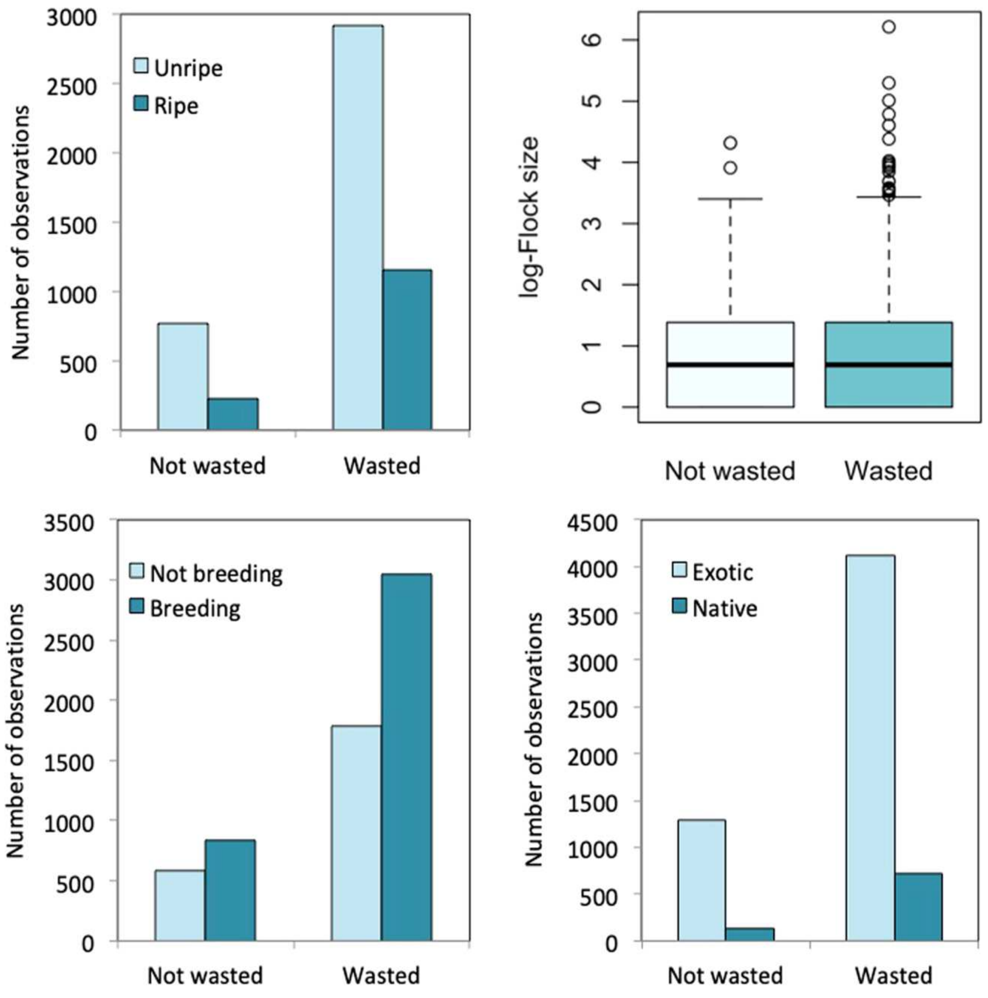

Figure 3. Representation of the food wasting occurrence (food wasted vs. food not wasted) in relation to the ripening stage of the fruit/seed (unripe/ripe), the log-flock size, the season when the observation was taken (breeding/non-breeding), and the origin of the plant (native/exotic) where the observation was taken.

Results obtained using experimental data showed that species size (i.e. average body mass, P7), food availability (i.e. fasting, P8) and conspecifics disturbance (i.e. number of individuals in the cage, P5) did not affect the proportion of food wasted (all p-values > 0.14, Supplementary Table S3). Finally, we also found that the total proportion of wasted fruits that were parasitized was very low (<4%, n = 176, P11).

Ecological functions of food wasting

By checking the amount of food wasted under the trees where parrots had been wasting food, we found that this was large in many cases, as expected (P12). We found an average (±SD) of 53.4 ± 52.2 wasted fruits and 42.0 ± 54.9 wasted seeds under the trees (Supplementary Table S4). The maximum number of seeds found under a single tree (239) was larger than the number of fruits (164).

The number of species that benefited from the food wasted by parrots was also large and widely distributed, supporting P13, including 86 species of birds, mammals, reptiles, fishes, and ants (Table 3) that widely ranged in body size (0.002–750 kg). Also, we detected 28 different species from 26 genera potentially acting as secondary dispersers of the fruits and seeds wasted, including ants, birds, mammals and reptiles. As predicted (P14), these species ranged from very small to very large body sizes, and their average dispersal distances were mainly large (>30 m), but also very large (>100 m) for two species.

Table 3 Number of species detected consuming or as secondary dispersers of the fruits wasted by parrots by taxonomy, functional group, body size and dispersal distance. *This is a conservative number of species due to the hard species identification.

		Food facilitation	**Seed dispersal**
Taxonomy	Species	86	27
	Genera	67	25
	Families	51	17
Group	Ants*	3	3
	Birds	53	13
	Mammals	27	9
	Reptiles	2	2
	Fishes	1	0
Body size	Very large (>10 kg)	13	2
	Large (>1 kg)	16	4
	Medium (>0.1 kg)	29	12
	Small (>0.01 kg)	23	6
	Very small (<= 0.01 kg)	5	3
Dispersal distance	Very large (>100 m)	—	2
	Large (>30 m)	—	11
	Medium (>10 m)	—	9
	Small (<= 10 m)	—	5

DISCUSSION

In this paper, we show that waste is not an anecdotic behaviour among parrots, but a widespread habit present in at least the 103 studied species. Waste is mainly focused on fruits and seeds, although it also involves other plant parts, and occurs throughout the year and through all the regions where parrots have native or introduced populations. We also show that waste has implications for other species that can forage or secondarily disperse wasted seeds and fruits. Thus, we can consider that parrots are interacting with plants along mutualism-antagonism continuums, as they can both prey upon several plant parts but also act as seed-dispersers, pollinators or plant healers (Montesinos-Navarro et al. 2017; Blanco et al. 2018).

Besides waste being a widespread behaviour in parrots, we found that the proportion of food wasted changed between species, suggesting that some ecological or evolutionary factor may be modulating this behaviour. However, our tests to disentangle the accidental or deliberate nature of waste were not conclusive. We found that parrots waste more food from non-native plant species than from native ones, maybe because they had a shorter co-evolutionary history to adjust their handling techniques to the fruits and seeds of these novel species. Also, exotic plant species are often located closer to human infrastructures and thus, waste may be a consequence of human disturbance (i.e. parrots suddenly flying away and dropping food when humans get close to them). We also found that waste is more frequent during the non-breeding than during the breeding season, which is probably related to the higher nutritional requirements that individuals have while raising chicks (Martin 1987). If individuals need to gather more food for themselves and their chicks during the same time, they may choose to reduce food waste to increase foraging efficiency, suggesting that waste may also be deliberate. Also, parrots seem to waste with a higher frequency low quality (i.e. unripe) fruits, showing some type of selectivity. However, we did not find differences in food waste in relation to species body size or food availability (i.e. fasting), suggesting that metabolic differences among species and food availability are not driving this behaviour. Finally, some studies had suggested that parrots might preferentially waste or consume parasitized fruits, modulating the effect of parasites on plant fitness (Selman et al. 2002; Symes and Perrin 2003). However, our observations did not show any preferential consumption of parasitized fruits.

Food wasted by parrots benefits many animal species, as seeds and fruits become more readily available and during a longer temporal window after being thrown from the tree by parrots. Also, wasted food is less often rotten or dry, as happens when food naturally falls from the trees. Parrots waste plenty of half-eaten fruits, reducing the original size of the fruit and breaking hard fruit parts, thus allowing their consumption by smaller species. For example, Douglas et al. (Douglas et al. 2013) found that the quantity of parrot frugivory increased habitat quality for Bananaquits (*Coereba flaveola*), because of parrot ability to open hard fruits and leave them partially consumed and thus available for other species. Besides, fruits become available for ground-dwelling species that otherwise cannot access the resource (as already suggested in (Galetti and Rodrigues 1992; Galetti et al. 1993; Martens et al. 2013)).

Fruits and seeds wasted by parrots can also be subject to secondary dispersal by many animals. This may be vital for some plant species, as many plants rely on secondary dispersal in their reproductive cycle (Chambers and MacMahon 1994; Vander Wall and Longland 2004). It is important to underline that even if many of the wasted fruits and seeds are unripe and partially consumed, a large proportion of them can ripen and germinate after dispersal (Barnett et al. 2012; Tella et al. 2016; 2019). Also, having seed dispersers with different ecological characteristics (e.g. home ranges, places to defecate, dispersing methods) may increase the chances of effective seed dispersal (Vander Wall and Longland 2004). The list of species either consuming food discarded by parrots or acting as secondary dispersers is very large, and includes many species from different taxonomic groups and with very different body sizes and dispersal distances. It is worth mentioning that our list is very conservative, as many of the species that we observed consuming the wasted fruits and seeds can also potentially disperse them. Thus, the impact of this wasteful behaviour on a large list of animal and plant species may be large given its universality.

Besides food facilitation and secondary seed dispersal, waste may have other ecological functions. If this behaviour has been maintained over the evolutionarily history of this old and diversified animal group (Toft and Wright 2015), it may be because it has some beneficial consequences for parrots (Blanco et al. 2018). One suggestion is that waste may benefit parrots by increasing the availability of high quality (e.g. large-sized, sugar-rich and nutrient-rich) fruits. In horticulture, it is widely known that such large high-quality fruits can be obtained through fruit and flower pruning (Link 2000; Hehnen et al. 2012). Interestingly, pruning needs to be directed to unripe fruits to affect the quality of the non-wasted fruits (Tukey and Einset 1938; Havis 1962; Dennis 2000), coinciding with our result that waste occurs with a higher frequency in unripe fruits. Moreover, fruit and flower pruning are also known to reduce gaps between fructifications (Stephenson 1981) or reduce biennial bearing (Hehnen et al. 2012; Dag et al. 2009; Seehuber et al. 2011). Thus, parrots may also be extending the fruiting period of the trees and increasing their predictability (i.e. shorter gaps between fructifications and transition from biennial to annual bearing). For any of these hypotheses to be possible, parrots need to be able to make intertemporal choices (i.e. sacrifice short-term satisfaction to obtain a higher reward in the future), which have already been detected for this bird group (Krasheninnikova et al. 2018). Overall, waste may have longer-time effects on wasted plants than expected, but further studies are needed to validate this hypothesis.

Besides the apparent negative effect that fruit and flower wasting may have for the plant, it is widely known that many plant species naturally produce more flowers and fruits than they can set (Stephenson 1981). The overproduction of juvenile fruits may be evolutionarily adaptive as these can satiate pre-dispersal fruit and seed predators (Janzen 1971a,b) and plants may be able to produce larger yields than average in occasional years of plentiful resources (Wilson and Price 1977; Udovic 1981). Plants may also compensate this overproduction by aborting flowers or fruits during the growth process36. As wasted fruits are preferentially unripe, their loss can be partially compensated by reducing fruit or flower abortion, reducing the negative effect of fruit thinning for the plant.

Waste may also have important consequences for the soil, as large amounts of organic matter accumulate over short time periods under a single tree. This behaviour may also expedite nutrient cycling, as wasted plant parts may enter the decomposition phase faster than if they were to stay in the tree for longer time periods (Blanco et al. 2018). Overall, our study wants to emphasize the universality of waste in parrots and the important implications this behaviour may have for the species involved (i.e. plants and parrots), but also show how other species benefit from the wasted food and for the functioning of the ecosystem.

Two specifications about our study need to be done before concluding. First, it is important to notice that the experimental data cannot be directly compared with what happens in the natural environment as the food provided and the way parrots obtain is markedly different. However, the waste experiment was designed to control for several factors that would be very challenging to account for in the wild. For example, it is very difficult to test among-species differences on the wild because the species are never found under the same circumstances (e.g., environmental conditions, food species). Another important factor that cannot be tested in the field but was easily addressed in the experiment was food availability. Therefore, the experiment offers complementary information to that provided by the data gathered in the field. Also, in our predictions

(Howe 1980; Bosch and Wedde 1981; Galetti and Rodrigues 1992; Galetti 1993; Symes and Perrin 2003), we assume that an individual wasting less food has a higher foraging efficiency than an individual wasting more food. However, it may be more efficient to feed by partially eating and wasting various fruits than to handle the same fruit for a long time, which will become smaller and more difficult to eat. This does not invalidate our predictions, as about half of the fruits and seeds wasted are intact (see Supplementary Table S3).

Despite the several aspects that deserve more research, this study adds to the growing evidence that parrots have a much more important role for the conservation of the ecosystems than previously thought (Blanco et al. 2015; Montesinos-Navarro et al. 2017). Some of the functions attributed to parrots, such as primary and secondary dispersal (Tella et al. 2015; Blanco et al. 2018; this study), may have a very important role in the current scenario of global change where tropical forests are being fragmented at high rates and forest recovery may depend on the efficiency of seed dispersal. However, many parrot species are highly endangered, with several species functionally extinct and many of the remaining species under strong human pressure (e.g., 28% of extant species are classified as threatened under IUCN46). Thus, management efforts to conserve parrot species should considerate the ecological interactions of food waste in the conservation planning strategies of habitat protection and population recovery (e.g. selection of priority areas for conservation and selection of release sites).

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SUPPLEMENTARY MATERIAL

Tables S1, S2, S3 and S4 (s*ee Supplementary Material Section 3-Chapter VIII*).

Datasets 1-5 (see link)

https://www.nature.com/articles/s41598-019-51430-3#additional-information

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SECTION 4:

NON-NATIVE PARROTS AND MANAGEMENT PLANS

THESIS DISCUSSION

The emergence of biotic interactions between non-native/invasive species and recipient community are expected as well as ultimately result in impacts on native species. This thesis assesses the role of biotic interactions on establishment and invasion successes for several non-native parrot species with native biota. Our results show that non-native parrots perform a wide range of interactions in different ecological contexts that assist their establishment and spread, which in turn result in ecological impacts together positive effects on both native and non-native biota. Rose-ringed parakeet outcompetes with recipient cavity nester community through aggressive interspecific interactions that influence on spatial distributions of its competitors. Mainly on one of its competitors, the greater noctule, that shows a worrying population decrease, so the viability of the largest greater noctule population worldwide is threatened. Whereas monk parakeet displays a role of ecosystem engineer that provides alternative nesting sites to recipient community in its invaded areas, assisting thus the establishment of both native and non-native tenants. In other scenarios, non-native parrots develop novel interactions with recipient community and behavioral innovations to overcome barriers from recipient environments. In this way, monk parakeet displays nesting association (i.e. commensalism) with a native species, white stork, to avoid higher predation pressure rates in its spread from urban to rural areas. While rose-ringed parakeet innovates nesting behaviors as response to shortage of nesting sites whereby a nesting association with another invasive species, monk parakeet, as well as a novel behavior as tree cavity excavator. Another novel interaction is showed by an incipient non-native population of orange-winged amazon that surprisingly overcomes mating shortage by hybridization with another non-native parrot species, scaly-headed parrot, to breed hybrid offspring. Moreover, a total of X non-native parrot species are involved in animal-plant mutualisms as seed dispersers through epizoochory and promote secondary dispersals by way of food wasting. However, most seeds dispersed seeds are from non-native/invasive plants, so synergic facilitations may occur between non-native species. Finally, between different management plans focused on rose-ringed parakeets the eradication by shooting is the most efficient action to address properly issues and conservation implications from invader, so this action should be also considered for other non-native/invasive parrot species. Therefore, this thesis highlights the importance of detecting biotic interactions and consequent impacts on native species to understand their role in biological invasions and implement feasible management plans.

Biotic interactions: Key factors for invasion success

The good invader

Much interest has been focused on different level factors (e.g. event, location and species) that are keys in the understanding of biological invasions and influence on the success of invasion process (Blackburn et al. 2011). Although an incorrect assessment of these factors may misunderstand the importance of different processes in each invasion stage, in which, biotic interactions are usually overlooked (Abellán et al. 2017). In this doctoral thesis, we focused on the most successful parrot invaders, rose-ringed and monk parakeets, to assess different biotic interactions showed by both invasive species with their respective recipient communities, which are determinant in their invasion success (Section 1 and 2).

Previous studies on rose-ringed parakeet record aggressive behaviors against its nesting competitors both in its native and invasive range (Lamba 1996; Strubbe and Matthysen 2009a; Strubbe et al. 2010; Orchan et al. 2013; Yosef et al. 2016). Its aggressiveness rate is associated with its highly dependence from available cavities in its breeding area, so competition pressure for this limiting resource is much greater between secondary cavity nesters (Newton 1994) and aggressive behaviors may be beneficial despite costs as energy spent and potential fatal encounters (Grether et al. 2013). In our study cases, rose-ringed parakeet is present in two different scenarios regarding the recipient cavity nester community, while the population located in Tenerife coexists with low densities and poor diversity of cavity nesters, consequently interspecific competition for nesting sites is nonexistent (Section 2), the population located in Seville disrupts on native cavity nester community more structured and diverse, through aggressions that have direct effects on its competitors such as, usurpation of nests, wounds and lethal interactions (Section 1). These negative interactions have consequences on spatial arrangement nests of other cavity nesters. Thus, we observed that rose-ringed parakeet successfully invades novel environments by means of two processes, whereby it exploits nesting resources poorly used by coexisting native species (i.e. opportunism hypothesis; Catford et al. 2009) or outcompetes other exploiters that share same preferences for nesting resource (i.e. competition hypothesis; MacArthur 1970). This paradox (Sol et al. 2012) is conditioned by recipient community structure which coexists rose-ringed parakeet in its invaded areas, so different local traits of recipient community may promote different responses from invaders and that finally determinate on the success of invasion process (Duncan et al. 2003; Blackburn et al. 2011).

However, other responses from invaders may arise under unfavorable environmental conditions such as the unavailability of nesting sites. Behavioral changes on the exploitation of limiting resources (e.g. food sources and nesting sites) are keys in the successful establishment of several invasive species, providing thus alternative resources that supply resource shortages (Cassey et al. 2004; Sol et al. 2005). We assessed how rose-ringed parakeet population established in Tenerife shows two different nesting innovations that increase the availability of nesting sites in the invaded area (Section 2). Although rose-ringed parakeet mainly breeds in tree cavities, it may also breed in cavities located in buildings or modify entrance sizes of preexisting cavities as response to saturation of available tree cavities (Lamba 1996; Yosef et al. 2016; Section 1). In our study case, the progressive saturation of tree cavities was caused by conspecific pairs in absence of interspecific competitors in the area. Consequently, several rose-ringed parakeet pairs developed two novel nesting strategies, as primary cavity nester and tenant of monk parakeet nests, to mitigate the shortage of available nesting sites. These behavioral innovations may involve additional costs (Snell-Rood 2013), such as more energy requirements to excavate own cavities and potential risks during the usurpation of monk parakeet nests (Wiebe et al. 2007; Grether et al. 2013), although the increasing number of available cavities compensate these costs that assist the invasion success of rose-ringed parakeet. Despite biotic interactions such as competition interactions together with own species traits such as behavioral flexibility, are frequently unexpected, it is unclear their role at local levels in invasion success (Holway et al. 2002; Vilà et al. 2005) although our results suggest that both factors positively affect on the invasion process of rose-ringed parakeet in different community and environmental contexts.

Native species, as both facilitators and deterrents of biological invasions

Albeit traits of recipient communities are considered as key factors that affect on the invasion success or invasibility degree (Catford et al. 2009; Saul et al. 2013), studies about resultant interactions of native species have been mainly focused on negative interactions in detriment of those positive for invasive species (Braga et al. 2018), so this bias involves a misunderstanding on the complexity of biotic interactions in biological invasions (Bruno et al. 2003; Le Roux et al. 2020). Invasive species may gain novel biotic interactions regarding their native geographical areas (Catford et al. 2009), so novel interactions of both types are expected together with their effects on invasion success. In the case of monk parakeet, we propose that opposite mechanisms as resultant of interactions with recipient communities may hugely determinate the establishment and spread of this invasive parrot species (Section 1 and 2).

The loss of natural enemies in their introduced ranges (i.e. enemy release hypothesis; Williamson and Griffiths 1996) lets some invasive species to invade successfully novel environments, when recipient community is not a ecological barrier for invasion process (Colautti et al. 2004; Catford et al. 2009). Nevertheless, native species also display enemy roles for invasive species and decrease their invasion success through negative interactions such as competition and predation, triggering a biotic resistance that controls invasive species populations (Elton 1956; Byers 2002). We assessed this enemy role via top-down regulative processes showed in the native raptor community that coexists with an monk parakeet population that is starting to spread into surrounding rural areas in Madrid (Section 2). Overall, rural environments mostly show larger diverse communities than urban areas (McKinney 2006), so likelihood of encounters between potential enemies is higher for invasive species (Catford et al. 2009). Spread patterns and spatial nest distribution of monk parakeet are shaped by presence of breeding areas of native raptors, avoiding thus greater concentrations located in rural environment, so predator community controls on prey population at local scales (Byers 2002; Carlsson et al. 2009). However, a native species, white stork, provides a protective nesting association that facilitates the establishment and spread of monk parakeet in rural areas. In this way, monk parakeet benefits of effective antipredatory defense of white storks when it builds its nests closely to their nests, which prevents higher predation pressure from raptors in rural areas. This commensalism by which an invasive species is benefited without reciprocity by a native species overcomes the biotic resistance from native predators and consequently assists the invasion success, hence, opposite interactions performed by native community enhance and decline biological invasions.

Additional negative interactions from native species were also observed in other study monk parakeet populations in which some native species parasite and despoil aggressively their nests (Section 1). This loss of nests has direct effects on breeding success of monk parakeets due to energy costs to rebuild nests, so a regular nest usurpations causes breeding failure (Prokop 2004) that finally decreases the invasion success. Although, this negative effect on monk parakeets is compensated by same or other tenant species through positive interactions such as commensalism and mutualism, enhancing thus the antipredator behavior of monk parakeet. These protective nesting associations trigger a cooperative defense between different species that concurrently benefits monk parakeets (Blanco and Tella 1997). As with nesting association between white storks and monk parakeets (Section 2), there is a balance between costs and benefits of biotic interactions from native community that affect on invasion success. We support that recipient community displays a double role in the success of biological invasions (Lodge 1993; Mitchell et al. 2006; Braga et al. 2018) in which invasive species do not only gain novel interactions with native species that provide advantages from novel mutualistic webs (Alpert 2006; Sax et al. 2007) but also negative effects from novel natural enemies (Biotic Resistance Hypotheses; Elton 1956). Therefore, this complexity of biotic interactions also has whether or not direct effects on native species (White et al. 2006), taking bidirectional ways regarding interaction types from invasive species (see below).

Impacts on the recipient community

A large spectrum between winners and losers

Disruption of invasive species entails a wide range of biotic interactions between invasive and native species that may trigger impacts on native biota (Ricciardi et al. 2013; Simberloff et al. 2013), although its detection is frequently lacking (Hulme et al. 2013) with little evidences are still present in the literature, especially scarce in vertebrates (Kumschick et al. 2013; Martín-Albarracín et al. 2015). This thesis recorded and assessed different biotic interactions in abroad invasion contexts that were mainly displayed by two invasive parrot species, rose-ringed and monk parakeets, although a total of X non-native parrot species also were recorded their interactions with native species (Section 1, 2 and 3).

Studies of interactions between rose-ringed and monk parakeets with recipient communities provided a complex net of interactions that whether or not benefits invaders and those species which they interact (Section 1). Thus, we assessed the impact through nesting competition by rose-ringed parakeet on cavity nester community, in which its aggressive behavior shown during its interspecific interactions that directly resulted in nesting usurpations and lethal encounters for several native species. Likewise, this competition pressure dismisses several species to cavity nests of low qualities, which are indirectly promoted to breeding failures (Newton 1994; 1998). Nevertheless, its aggressions do not only were focused on nesting competitors but also predators that may depredate on adults (e.g. raptors) or on chicks and eggs (e.g. corvids and rats), showing an effective antipredator behavior in this encounters (Section 1 and 2). The nesting protection provided by rose-ringed parakeet benefits several native species after a reduction of predation pressure in their breeding areas (Blanco and Tella

1997; Lima 2009), although benefits of this positive effect may be also insufficient for native community. On the one hand, impacts by competition may be too severe to relieve negative consequences of competition pressure, chiefly for threatened species or with incipient conservation risks (Dueñas et al. 2018) such as greater noctules and lesser kestrels, that are more sensible to ecological disruptions. On the other hand, this protective nesting association may be provided to other invasive species, such as monk parakeets, so invasional meltdown processes may arise and assist invasion processes of both invasive species, increasing thus the emergence of impacts on native community and environment (Simberloff and Von Holle 1999). Moreover, this double scenario between competition and antipredatory defense may unbalance after the population growth of rose-ringed parakeet that improves its impacts on the rest of cavity nester community.

In the case of facilitation of nesting sites showed by monk parakeets and, to a lesser extent by rose-ringed parakeet, is a positive effect on recipient community, mostly secondary cavity nester species (Section 1 and 2). Monk parakeet builds its own nests that aggregate in colonies (Senar et al. 2016) and are exploited by other tenant species in its native range (Martella et al. 1985; Wagner 2012), so we assume that monk parakeet also displays this role of ecosystem engineer in its introduced geographical distribution (Section 1). This facilitation has positive effects on populations of native species (Rodriguez 2006) due to the increasing availability of nesting sites, a limiting resource both secondary cavity nesters and those species that could not previously colonize unsuitable environments (Jones et al. 1997; Martin and Eadie 1999). Recorded tenant species develop commensalistic and mutualistic interactions with their host in which they gain novel nesting resources that provide suitable breeding conditions such as thermoregulation and isolation (Navarro et al. 1992), assisting thus breeding success of these tenant native species. Besides, as in the previous case of rose-ringed parakeet (Section 1 and 2), different tenant displays antipredatory behaviors against nest predators and that secondarily benefits on rest of tenant species established in the interspecific colony (Blanco and Tella 1997; Lima 2009). These synergetic effects positively affect on diversity of native tenants, so incorporations of rare and threatened species are also facilitated by monk parakeets in their recipient environments (Tracey and Miller 2018). However, this growing biodiversity also is owing to the adding of non-native and invasive species, hence, recorded benefits are also exploited by these species and invasional meltdown processes may arise, impacting thus recipient community and environment. Moreover, these non-native species, including monk parakeet host, may introduce novel parasites (Mori et al. 2015; Briceño et al. 2017; Ancilloto et al. 2018) on existing parasite load in monk parakeet colonies with potential negative effects on breeding success of native tenant species. Consequently, the facilitator role of monk parakeets in their recipient communities causes direct positive effects but also indirect impacts on native species. In addition, both invasive parrot species as well as a total of X non-native parrot species also provided food resources during their foraging activities to different taxonomic groups, both native and non-native species, in their introduced geographical areas (Section 3). These species could not exploit these novel food sources without previous action of non-native parrots, so they benefits of this positive interaction (i.e. food facilitation) that provides them additional food resources, thereby enhancing their fitness and population growth (Boucher 1982). Likewise, we consider another ecological effect that arise from this food facilitation, the secondary seed dispersal (see below).

Overall, we suspect that opposite processes, negative and positive interactions, operating on the same scale have effect on community-level processes in complex feedbacks between impacts and benefits for native species (Blackburn et al. 2013). Disruption of non-native species is one of the key drivers regulating the biodiversity and that induces changes on community dynamics (Clavero and García-Berthou 2005; Vilà et al. 2011). In this dynamic context, positive interactions provided by non-native species may be completely sidelined across different invasion stages as well as under increasing pressure from larger populations of non-native species. Therefore, more long-term studies focused in biotic interactions are necessary to assess properly its complexity and effects on native species and communities.

Animal-plant interactions: The overlooked effects of parrots

Parrots are a diverse group of frugivorous generalists that exploit a high diversity of plants, likewise all plant parts in their different maturation stages. Widely considered as seed predators, parrots have been mostly neglected of their mutualistic roles in studies of animal-plant interactions (Blanco et al. 2015, Montesinos-Navarro et al. 2017), although their role as seed dispersers has been supported in recent studies, both as primary seed dispersers (Tella et al. 2015, Blanco et al. 2018). However, the implication of parrots in other seed dispersal mechanisms such as epizoochory and secondary seed dispersal, are completely unknown. This thesis assessed both seed dispersal mechanisms to evaluate its incidence between different non-native parrot species and their recipient plant communities (Section 3).

Although seed predation shown by non-native parrots impacts on fitness of depredated plants (Blanco et al. 2018), we recorded widespread cases of seed dispersals that involved a large number of parrot and plant species that compensate negative effects from seed predation. Thus, parrots displays the role of primary seed dispersers through epizoochory as well as promoters of secondary dispersal by means of food facilitation. It is known both native and non-native frugivorous vertebrates may disperse introduced plants (Traveset and Richardson 2014, Molefe et al. 2020). Besides, non-native plant species outcompete native flora for attention of potential seed dispersers (Traveset and Richardson 2014). Our observations support that non-native parrots show a high preference for non-native plants, so these mutualistic interactions may trigger negative cascading effects on native plant community and additional indirect effects caused by secondary dispersers facilitated by non-native parrots. Consequently, these synergetic processes assist biological invasions likewise increase the magnitude of impacts caused by invasive parrot species by means of invasional meltdown processes.

Role of epizoochory in mutualistic networks is poorly known, especially in terrestrial birds (Costa et al. 2014, van Leeuwen et al. 2020), so future studies should focus on the retention time of seeds on parrot's body surfaces to record the dispersal distances. Parrots meet certain conditions that assist seed retention, such as long living and wide range of movement, both spatial and seasonal, in their foraging areas and enhancing thus epizoochory effectiveness (Gorb et al. 2020). These long retention times could be potentially over than those recorded in endozoochory (van Leeuwen et al. 2020) and, consequently, dispersed at larger distances. Additional studies focused on interference of non-native plants with different zoochory mechanisms could provide information about the effectiveness of seed dispersal between native and non-native species.

Concerning non-native parrots: Conservation implications

International wild-life trade is source of 16.6% living parrot species show non-native populations out their natural geographical areas (Menchetti and Mori 2014). Despite prevention of establishment non-native species is the most important step to avoid biological invasions (Wittenberg and Cock 2001), such as conservation efforts to ban and stop the traffic of wild-caught parrots since last decade (Cardador et al. 2019), when facing with non-native populations already established only rapid responses with effective management actions may resolve their associated issues (Wittenberg and Cock 2001; Edelaar and Tella 2012). In Section 4, we assessed the efficacy and feasibility of different methods and management actions focused on an invasive population of rose-ringed parakeet, regarding a time window of action that shows different impact degrees on population size of invader.

Our analysis of two alternative methods of management, removal of individuals or clutches, showed the most effective method is removal of individuals from the wild, likewise, eradication management actions are mandatory. Due to its high breeding success (Strubbe and Matthysen 2009b), rose-ringed parakeet is able to recover shortly its population after management actions, hence, control actions do not address feasibly stable population sizes that minimize impacts of invader at long-terms. Besides, our simulations focused on different methods of removing individuals from the wild, trapping and shooting, their success depended of population size of rose-ringed parakeet, being shooting method more effective for large population sizes and rapid to achieve the eradication. To date, shooting has been demonstrated its effectiveness in total eradication focused in invasive rose-ringed parakeet populations (SIF 2017; Bunbury et al. 2019; Saavedra and Medina 2020) as well as on monk parakeets (Esteban 2016). We know eradication programs have little social support, mostly if focused invasive species is charismatic such as parrots (Crowley et al. 2019), to the extent that some management plans have failed (Van Bael and Pruett-Jones 1996; Avery and Tillman 2005). Growing "invasive species denialism" caused by skepticism from interest vested groups out of scientific consensus (Russell and Blackburn 2017) jeopardizes the implementation of feasible and effective management plans to address issues of biological invasions. Along these lines, consensual discussions focused on approaches of invasive species managements should be built in scientific evidences to inform correctly citizens in awareness campaigns (Blackburn et al. 2010).

Both recorded and potential impacts that have observed do not only in rose-ringed and monk parakeets, but also in other non-native parrots (Menchetti and Mori 2014; White et al. 2019; Section 1 and 3) should be concerned, employing monitoring programs, especially in incipient non-native populations. After introduction, non-native species overcome different barriers to establish successfully in novel environments in which poorly known factors determinate the success, complicating thus its prediction (Kolar and Lodge 2001; Blackburn et al. 2011). Thus, non-native parrots displays unpredictable behaviors and interactions with native community that complicate predictions focused on their establishment success (Section 2). For instance, we recorded a declining non-native population of orange-winged parrot overcomes the mating shortage through successful hybridization with another non-native parrot species, breeding healthy offspring that reduces Allee effects (Courchamp et al. 1999) and rescues this incipient population (Section 2). Therefore, we suggest more long-term studies focused on biotic interactions to design feasible practices and policies that anticipate widespread emergence of impacts as well as unexpected effects that assist the invasion success.

Final remarks

This thesis provides strong evidences that non-native/invasive parrots display interactions that may cause negative and positive effects on different recipient communities, in particular, impacts are more concerning when target on threatened species. Although some native species are benefited by introduced parrots, potential impacts may emerge after emergence of synergetic effects of invasive/non-native species that disrupt dynamic community. Finally, this thesis assesses the role of biotic interactions in the success of biological invasions in which recipient community may both facilitator and deterrent. Even though predictions for global biodiversity in the next century are no good, there are still opportunities to address it through better policies (Pereira et al. 2010), so it is encouraging that scientific studies provide more knowledge to engage this global ecological disaster. We hope that our research modestly achieves this goal and evidently, more studies focused in biotic interactions are needed to reveal their role in biological invasions through holistic approaches.

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THESIS CONCLUSIONS

1. Non-native parrot species interact on different scales with their respective recipient communities and environments present in their introduced areas. These biotic interactions are both gained and modified regarding those biotic interactions already showed in their native geographical areas. Novel interactions assist the establishment and spread of several parrot species in their introduced areas as well as trigger impacts on native species by invasive species.
2. The rose-ringed parakeet (*Psittacula krameri*) aggressively outcompetes for nesting sites and disrupts the native cavity nester community, affecting on spatial nest distribution of its competitors. It is considerable significant this negative effect on conservation-reliant species such as, the lesser kestrel (*Falco naumanni*) and greater noctule (*Nyctalus lasiopterus*). However, its aggressive behavior also provides effective anti-predatory defense of nesting areas, so it benefits some cavity nesters that breed near rose-ringed parakeet nests.
3. This situation for greater noctule (classified as Vulnerable) is acutely alarming for viability of its largest population worldwide, in which the growing number of rose-ringed parakeet nests promotes more lethal encounters for greater noctule. Moreover, the severe declining of its available refuges alters its social dynamics, displacing them thus to unsuitable nesting conditions and the stochasticity.
4. The monk parakeet (*Myiopsitta monachus*) as ecosystem engineer facilitates alternative nesting sites to recipient communities in its invaded areas through own built colonies, resulting thus in a "nest web" in which monk parakeets positively interacts with a wide diversity of tenant species, both native and non-native.

5. Tenant species show different interaction degrees with host monk parakeets (i.e. mutualism, commensalism, inquilism and parasitism) and although it may lose nests after aggressive occupation by tenants, it also benefit of their anti-predator behavior. While the growing availability of nesting sites assists the growth and establishment of native species, especially on rare species, likewise several invasive tenant species are benifet, so invasional meltdown processes may arise.

6. Native species influence on invasion success of monk parakeets in two directions. On one hand, recipient raptor community shows biotic resistance against the spread of monk parakeet on rural areas where its predation pressure is stronger than in urban areas. On the other hand, the white stork (*Ciconia ciconia*) provides monk parakeet an anti-predatory refugee through a commensalist nesting-association that assists its spread on rural environment.

7. As barrier from environment, shortage of nesting sites are overcome by rose-ringed parakeet via behavioral flexibility that results in two nesting innovations (i.e. as primary cavity nester and as tenant species), enhancing thus its fitness as well as assisting invasion process.

8. Novel interactions emerge due to nesting innovations performed by rose-ringed parakeet and consequently benefits other coexisting species. Invasive monk parakeet benefits on anti-predatory behavior by tenant rose-ringed parakeets established in their colonies, while some native cavity nesters may nest in these excavated cavities.

9. Incipient non-native populations with a low propagule pressure and population stagnation, such as Orange-winged amazon (*Amazona amazonica*), may overcome Allee effects by means of hybridization, which in turn, promotes a population rescue and consequently assists the success in early stages of establishment.

10. Non-native parrots conserve their role as plant mutualists in their introduced ranges through different seed dispersal mechanisms, such as epizoochory, estomatochory and secondary seed dispersal. Novel facilitation interactions between non-native parrots and other animal species provide new food resources through wasting food, both native and non-native fauna, likewise secondary seed dispersals.

11. Different seed dispersal mechanisms performed by non-native parrots are mostly biased to non-native/invasive plant species. These mutualistic interactions might disrupt on native plant community and trigger invasional meltdown processes.

12. Owing to recorded and potential impacts and on native community performed by non-native parrots, especially rose-ringed parakeet, management actions are urgently required. Not only are necessary the prevention and bans on international wildlife trade and possession of these species, but also effective control and eradication plans to deal already established populations.

13. Removing feral individuals is the most effective method to control or eradicate non-native parrot populations. Eradication is more efficient than control because success of management depends of long-term fluctuant factors such as public resources and social support. While trapping is suitable for small non-native parrot populations, eradication plans by mean of shooting is the most effective and efficient action, to address small and large populations.

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"A menudo, al leer un libro uno siente que el autor hubiera preferido pintar en lugar de escribir; uno puede sentir el placer que deriva de describir un paisaje o a una persona, como si estuviera pintando lo que está diciendo, porque en el fondo de su corazón habría preferido usar pinceles y colores."

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SUPPLEMENTARY MATERIAL

SUPPLEMENTARY MATERIAL SECTION 1-CHAPTER III

Appendix S1. Explanatory variables for occupation of cavities by noctules from Nest-site competition and killing by invasive parakeets cause the decline of a threatened bat population

cavity	occupied	size	height (in m)	nndk (in m)	agregk	nndn (in m)	agregn	year
1	0	3	5.4	6.17	129.05	96.34	41.47	2013
2	0	1	9	4.42	135.29	43.82	44.17	2013
3	0	2	12.6	45.19	133.62	12.58	44.03	2013
4	1	2	9	33.44	134.54	70.48	43.30	2013
6	0	3	9.9	17.67	136.78	34.18	45.75	2013
7	0	3	18	17.67	136.78	34.18	45.75	2013
9	0	2	5.4	8.63	113.69	22.61	37.75	2013
10	0	3	7	16.94	114.50	28.84	38.08	2013
11	0	2	12.6	16.94	114.50	28.84	38.08	2013
13	0	1	14.4	9.23	136.25	26.51	45.08	2013
14	0	3	4.5	9.23	136.25	26.51	45.08	2013
17	0	3	7.2	13.06	120.88	77.59	40.03	2013
18	0	1	7.2	21.96	118.89	64.10	39.68	2013
19	0	2	10.8	21.96	118.89	64.10	39.68	2013
20	0	2	3.6	81.00	117.39	64.37	40.07	2013
21	0	2	14.4	81.00	117.39	64.37	40.07	2013
22	0	2	5.4	78.08	119.92	37.75	41.09	2013
23	0	2	7.2	70.28	121.16	26.61	41.44	2013
24	0	2	7.2	70.28	121.16	26.61	41.44	2013
25	0	3	13.5	36.44	122.45	29.88	41.29	2013
26	0	3	19.8	36.44	122.45	29.88	41.29	2013
27	0	2	6.3	40.37	126.83	31.15	42.66	2013
28	0	1	6.3	40.37	126.83	31.15	42.66	2013
29	0	1	9	7.41	136.47	24.70	45.34	2013
30	0	2	30.6	7.41	136.47	24.70	45.34	2013
32	0	1	6.5	39.20	126.99	30.98	42.72	2013
33	0	2	9	38.33	129.12	37.79	44.12	2013
34	0	1	9	38.33	129.12	37.79	44.12	2013
35	1	2	12.6	65.73	125.87	22.84	41.93	2013
36	0	1	4.5	65.73	125.87	8.10	41.94	2013
37	0	2	10.8	68.44	125.50	3.99	42.80	2013
38	0	1	4.5	72.11	125.51	7.36	42.93	2013
39	0	1	4.5	54.23	127.27	16.74	43.47	2013
40	0	2	9	50.33	123.89	19.17	41.91	2013
41	0	2	15.3	50.33	123.89	19.17	41.91	2013
42	0	1	6.3	50.33	123.89	19.17	41.91	2013
43	0	3	8.1	79.72	127.27	26.65	44.30	2013
45	0	1	12.6	54.58	130.13	58.81	45.00	2013

46	0	1	9	54.58	130.13	58.81	45.00	2013
47	0	1	10.8	38.34	129.91	50.23	44.54	2013
48	0	2	5.4	111.14	121.64	39.94	42.88	2013
49	0	1	5.4	111.14	121.64	39.94	42.88	2013
50	0	1	5.4	79.47	123.94	47.27	43.97	2013
51	0	1	5.4	91.05	123.72	29.51	43.61	2013
52	0	1	9	91.05	123.72	29.51	43.61	2013
53	0	1	7.2	101.01	123.21	23.64	43.31	2013
54	0	2	9	37.79	128.16	63.44	45.42	2013
55	0	1	9.9	58.37	124.52	93.78	44.93	2013
57	0	1	10.8	55.64	122.50	107.49	44.79	2013
58	0	2	15.3	7.56	137.37	4.42	45.68	2013
59	0	3	9.9	7.56	137.37	4.42	45.68	2013
60	0	1	6.3	44.80	123.31	61.32	45.86	2013
61	0	1	10.8	47.27	122.94	65.28	45.69	2013
62	0	1	12.6	53.53	122.40	62.58	45.61	2013
63	0	1	10.8	56.54	121.88	58.80	45.57	2013
65	0	2	12.6	38.29	122.92	25.17	46.51	2013
67	0	2	18.8	43.38	122.84	11.93	46.90	2013
68	0	1	10.8	48.39	122.75	13.92	47.05	2013
69	0	1	13.5	48.39	122.75	13.92	47.05	2013
70	0	2	8.1	34.60	124.05	3.60	46.32	2013
71	1	2	11.7	34.60	124.05	80.86	46.31	2013
72	0	3	11.7	34.60	124.05	1.00	46.31	2013
73	0	2	12.6	28.53	137.89	3.60	45.46	2013
74	0	1	7.2	28.53	137.89	9.00	45.46	2013
75	0	1	9.9	28.53	137.89	6.30	45.46	2013
76	0	1	10.3	28.53	137.89	5.90	45.46	2013
78	1	2	16.2	28.53	137.89	28.04	45.46	2013
79	0	1	9.9	58.91	120.74	39.30	45.85	2013
80	0	2	9.9	58.91	120.74	39.30	45.85	2013
81	0	2	4.5	52.08	121.50	38.81	45.94	2013
83	0	1	17.1	52.08	121.50	38.81	45.94	2013
84	0	2	12.6	52.08	121.50	38.81	45.94	2013
85	0	3	13.5	52.08	121.50	38.81	45.94	2013
86	0	1	9	52.78	121.60	45.50	45.80	2013
87	0	2	14.4	52.78	121.60	45.50	45.80	2013
88	0	2	14.9	52.78	121.60	45.50	45.80	2013
89	0	3	14	52.78	121.60	45.50	45.80	2013
90	0	1	8.1	18.88	125.90	42.74	47.00	2013
91	0	2	9.9	18.88	125.90	42.74	47.00	2013
92	0	2	16.2	23.67	128.36	83.93	46.55	2013
93	0	3	10.8	23.67	128.36	83.93	46.55	2013
94	0	3	10	23.67	128.36	83.93	46.55	2013
95	0	3	9	23.67	128.36	83.93	46.55	2013
96	0	2	18	11.84	127.99	80.94	46.67	2013

97	0	2	21.6	11.84	127.99	80.94	46.67	2013
98	0	1	11.7	16.57	129.18	87.71	46.13	2013
99	0	2	8.1	16.57	129.18	87.71	46.13	2013
100	0	2	8.5	16.57	129.18	87.71	46.13	2013
101	0	2	20.7	16.20	131.93	55.45	47.15	2013
102	0	2	18	21.67	127.27	58.06	47.15	2013
103	0	2	13.5	12.70	130.84	32.87	48.89	2013
104	1	2	18	7.41	137.51	28.04	44.79	2013
105	0	2	18	14.92	130.52	33.64	48.96	2013
106	0	3	10.8	40.08	127.64	39.40	48.72	2013
107	0	2	14.4	40.08	127.64	39.40	48.72	2013
108	0	3	16.2	39.36	128.17	33.24	48.91	2013
109	0	3	7.2	39.36	128.17	33.24	48.91	2013
110	0	1	12.6	6.18	133.57	17.52	50.74	2013
111	0	1	13	6.18	133.57	17.52	50.74	2013
112	0	2	16.2	6.18	133.57	17.52	50.74	2013
114	0	1	18	3.99	133.52	20.75	50.81	2013
115	0	2	18	3.99	133.52	20.75	50.81	2013
116	0	3	12.6	2.37	133.66	19.65	50.81	2013
117	0	2	15.3	2.37	133.66	19.65	50.81	2013
119	1	2	12.6	9.03	135.58	9.03	49.55	2013
120	0	3	17.1	19.05	136.62	26.98	49.67	2013
121	0	2	13.5	19.05	136.62	26.98	49.67	2013
122	0	3	14	19.05	136.62	26.98	49.67	2013
123	0	3	6.3	11.97	137.13	28.76	49.81	2013
125	0	1	5.4	16.57	136.79	34.08	49.48	2013
126	0	3	16.2	16.57	136.79	34.08	49.48	2013
127	0	2	9	60.84	131.45	84.27	43.51	2013
128	0	3	16.2	7.41	137.23	31.71	49.65	2013
129	0	2	5.4	5.75	137.29	31.35	49.58	2013
130	0	3	23.5	5.75	137.29	31.35	49.58	2013
131	0	2	21.6	5.77	137.71	35.54	48.95	2013
133	0	1	7.2	17.69	138.22	29.98	48.03	2013
134	0	2	10.8	17.69	138.22	29.98	48.03	2013
135	0	2	11.7	58.19	124.79	64.86	49.37	2013
136	0	1	12.6	58.19	124.79	64.86	49.37	2013
137	0	3	7.2	58.19	124.79	64.86	49.37	2013
139	0	3	19.8	58.19	124.79	64.86	49.37	2013
140	0	3	9	26.67	123.34	33.39	47.75	2013
141	0	2	15.3	40.77	121.06	6.30	48.52	2013
142	1	1	21.6	40.77	121.06	31.32	48.51	2013
145	0	2	18	12.70	122.03	63.29	47.91	2013
148	0	3	15.3	63.29	119.13	54.26	47.99	2013
149	0	2	6.3	44.97	133.61	72.71	45.01	2013
150	0	3	15.3	44.97	133.61	72.71	45.01	2013
151	0	3	7.2	59.29	114.81	51.38	48.30	2013

152	0	3	8	59.29	114.81	51.38	48.30	2013
153	0	2	16.2	59.29	114.81	51.38	48.30	2013
154	0	2	14.4	59.29	114.81	51.38	48.30	2013
155	0	3	10.8	51.78	115.51	50.62	48.49	2013
156	0	3	14.4	44.50	116.23	50.62	48.64	2013
157	0	2	6.3	44.58	117.00	27.53	49.21	2013
158	1	2	9.9	31.64	120.05	4.50	48.32	2013
160	0	2	9	31.64	120.05	0.90	48.33	2013
161	0	2	9.9	31.64	120.05	1.00	48.33	2013
162	1	2	14.4	31.64	120.05	4.50	48.32	2013
163	0	1	15	31.64	120.05	0.60	48.33	2013
164	0	2	14.4	31.64	120.05	1.00	48.33	2013
165	0	2	13.5	29.98	120.62	0.30	47.53	2013
166	1	2	13.8	29.98	120.62	4.20	47.53	2013
167	1	2	18	29.98	120.62	4.20	47.52	2013
168	1	2	27	29.98	120.62	7.59	47.53	2013
169	0	2	29.5	29.98	120.62	2.50	47.54	2013
170	0	3	9.9	25.66	121.36	7.10	50.66	2013
171	0	3	12.6	6.96	122.99	2.40	49.84	2013
172	1	2	15	6.96	122.99	25.99	49.84	2013
173	1	1	17.1	34.75	122.16	13.86	49.81	2013
174	0	2	25.2	34.75	122.16	8.10	49.82	2013
175	0	1	30.6	34.75	122.16	13.50	49.82	2013
177	0	1	12.6	39.81	133.38	64.64	44.28	2013
178	0	2	12.6	39.81	133.38	64.64	44.28	2013
179	0	2	11.7	26.51	123.48	8.10	48.04	2013
180	1	2	19.8	26.51	123.48	2.20	48.01	2013
181	0	1	21.6	26.51	123.48	0.40	48.01	2013
182	1	3	22	26.51	123.48	2.20	48.01	2013
183	1	2	26.1	26.51	123.48	4.10	48.01	2013
185	0	2	10.8	22.17	123.84	4.79	51.02	2013
186	0	3	13.5	22.17	123.84	4.79	51.02	2013
188	0	3	9.9	37.62	122.59	15.74	49.98	2013
189	0	3	9.9	33.64	122.45	16.31	50.01	2013
190	0	1	31.5	44.28	128.83	36.30	50.10	2013
191	0	1	9	68.74	124.24	68.74	44.41	2013
192	0	3	14.4	28.49	128.57	41.57	51.25	2013
196	0	2	7.2	9.03	127.64	17.30	51.20	2013
197	0	2	8.1	9.03	127.64	17.30	51.20	2013
198	0	2	16.2	9.03	127.64	17.30	51.20	2013
199	0	2	9.9	9.03	127.64	17.30	51.20	2013
200	0	1	9.9	6.29	131.63	66.91	42.42	2013
201	0	2	14.4	6.29	131.63	66.91	42.42	2013
203	0	1	18	16.17	137.22	25.19	47.11	2013
205	0	2	21.6	17.82	128.35	17.69	51.19	2013
206	0	2	23.4	17.82	128.35	17.69	51.19	2013

207	0	1	6.3	21.21	128.86	17.26	51.06	2013
208	0	2	10	21.21	128.86	17.26	51.06	2013
209	0	2	16.2	21.21	128.86	17.26	51.06	2013
210	0	2	13.5	16.17	129.57	11.53	51.15	2013
211	0	2	14	16.17	129.57	11.53	51.15	2013
212	0	1	13.5	9.23	130.03	4.73	51.11	2013
213	0	1	14.4	9.23	130.03	4.73	51.11	2013
214	0	3	9	9.23	130.03	4.73	51.11	2013
215	0	2	10.8	13.03	129.92	8.24	51.16	2013
216	0	2	16.2	13.03	129.92	8.24	51.16	2013
217	0	2	23.4	13.03	129.92	8.24	51.16	2013
218	0	1	13.5	4.79	130.41	3.48	50.10	2013
219	1	2	21.6	4.79	130.41	3.48	50.09	2013
221	0	2	13.5	4.79	130.41	3.48	50.10	2013
223	0	1	10.8	7.59	130.64	4.74	51.13	2013
224	0	3	25.2	7.59	130.64	4.74	51.13	2013
226	1	1	10.8	40.50	131.92	38.81	50.28	2013
227	1	2	15.3	3.99	130.31	3.48	50.04	2013
228	0	1	12.6	23.30	136.71	26.04	46.93	2013
229	0	3	6.3	13.76	125.24	16.55	50.79	2013
230	0	2	23.4	13.76	125.24	16.55	50.79	2013
231	0	2	10.8	13.76	125.24	16.55	50.79	2013
232	0	3	13.5	5.77	124.01	22.40	50.83	2013
234	0	3	14.4	13.92	123.39	16.49	50.82	2013
236	0	3	13.5	28.20	122.33	12.35	50.76	2013
237	0	1	9	28.20	122.33	12.35	50.76	2013
238	0	2	21.6	28.20	122.33	12.35	50.76	2013
240	0	3	5.4	38.76	120.70	7.20	49.53	2013
241	0	2	23.4	38.76	120.70	9.23	49.53	2013
242	1	3	12.6	38.76	120.70	9.23	49.52	2013
243	0	3	7.2	41.72	119.82	9.03	49.31	2013
244	1	3	18	41.72	119.82	9.03	49.30	2013
245	0	1	25.2	41.72	119.82	7.20	49.31	2013
246	1	2	27	42.62	119.19	9.03	49.10	2013
247	0	3	9	42.62	119.19	9.03	49.12	2013
248	0	3	7.2	12.80	125.18	57.49	49.47	2013
249	0	3	19.8	12.80	125.18	57.49	49.47	2013
250	0	2	28.8	12.80	125.18	57.49	49.47	2013
251	0	3	10.8	12.80	125.18	57.49	49.47	2013
255	0	2	8.1	3.48	124.59	60.77	49.14	2013
258	0	2	9	14.84	124.48	55.68	49.49	2013
259	0	2	16.2	14.84	124.48	55.68	49.49	2013
263	0	2	10.8	35.78	136.05	40.50	46.38	2013
264	0	1	7.2	15.95	122.75	41.43	48.95	2013
265	0	2	12.6	15.95	122.75	41.43	48.95	2013
266	0	2	8.1	27.09	121.22	31.39	49.21	2013

268	0	2	12.6	15.47	124.45	31.46	50.23	2013
269	0	2	7.2	15.47	124.45	31.46	50.23	2013
270	0	1	9	19.50	120.98	34.75	49.30	2013
272	0	2	7	14.84	120.75	36.91	49.34	2013
273	0	2	8.1	69.34	114.40	46.26	48.30	2013
274	0	2	10.8	69.34	114.40	46.26	48.30	2013
275	0	2	14.4	69.34	114.40	46.26	48.30	2013
276	0	2	10.8	69.34	114.40	46.26	48.30	2013
277	0	2	9.9	124.35	108.62	56.81	46.12	2013
278	0	3	9	124.35	108.62	56.81	46.12	2013
279	0	3	12.6	129.42	108.46	61.39	46.07	2013
280	0	3	12.6	65.92	113.20	16.55	47.50	2013
281	0	2	10.8	65.92	113.20	16.55	47.50	2013
283	0	3	9	42.75	135.31	39.69	46.39	2013
284	0	1	7.2	62.01	113.97	9.00	47.05	2013
285	0	2	9.9	62.01	113.97	6.30	47.04	2013
286	1	2	16.2	62.01	113.97	12.35	47.04	2013
289	1	2	26.1	68.08	114.33	22.60	47.31	2013
290	0	1	27	83.29	113.51	17.77	48.06	2013
293	0	2	10.8	105.55	110.17	39.40	46.71	2013
294	0	2	16.2	97.03	111.55	28.99	47.29	2013
296	0	2	27	97.03	111.55	28.99	47.29	2013
297	0	1	13.5	116.09	110.84	49.99	47.04	2013
299	0	1	12.6	118.84	110.64	54.18	46.96	2013
300	0	3	19.8	118.84	110.64	54.18	46.96	2013
301	0	1	4	66.30	116.59	26.11	49.21	2013
302	0	2	5.4	83.22	115.59	38.05	48.84	2013
304	0	1	4	78.00	116.33	36.69	49.10	2013
305	0	1	5.4	68.51	116.10	25.89	48.98	2013
306	0	2	7.2	68.51	116.10	25.89	48.98	2013
307	0	1	4	74.59	115.36	24.30	48.74	2013
308	0	1	5.4	69.90	114.96	12.80	48.57	2013
309	0	2	7.2	69.90	114.96	12.80	48.57	2013
310	0	1	4	65.90	114.99	7.98	48.55	2013
311	0	2	5.4	65.90	114.99	7.98	48.55	2013
312	0	1	8.1	63.01	114.16	8.24	48.16	2013
313	0	2	8.1	63.01	114.16	8.24	48.16	2013
315	1	2	25.2	53.58	114.63	1.00	45.18	2013
316	1	3	25.2	53.58	114.63	1.00	45.18	2013
317	0	2	9.9	53.58	114.63	8.10	45.21	2013
318	1	2	18	53.58	114.63	7.20	45.18	2013
321	1	2	20.7	41.72	115.83	13.86	47.41	2013
324	0	2	23.4	27.95	117.33	14.25	48.76	2013
327	0	2	12.6	66.69	133.33	60.64	45.75	2013
328	0	2	7	66.69	133.33	60.64	45.75	2013
329	0	2	12.6	66.69	133.33	60.64	45.75	2013

331	0	3	5.4	26.67	117.69	19.45	49.04	2013
332	0	2	23.4	26.67	117.69	19.45	49.04	2013
333	0	3	16.2	19.65	118.83	30.55	49.38	2013
334	0	2	18	19.65	118.83	30.55	49.38	2013
337	0	2	27	26.21	135.75	35.63	50.76	2013
339	0	1	16.2	26.98	135.67	39.81	50.76	2013
340	0	1	16.2	36.54	135.37	25.62	50.68	2013
341	0	1	19.8	36.54	135.37	25.62	50.68	2013
342	0	2	18	36.54	135.37	25.62	50.68	2013
343	0	1	12.6	14.99	136.48	22.78	50.50	2013
344	0	3	15.3	8.10	135.73	8.24	50.62	2013
345	0	2	17.1	8.10	135.73	8.24	50.62	2013
346	0	2	12.6	8.10	135.73	8.24	50.62	2013
347	0	2	6.3	34.67	135.69	28.53	46.83	2013
348	0	2	8.1	34.67	135.69	28.53	46.83	2013
349	0	3	6.5	34.67	135.69	28.53	46.83	2013
351	0	1	9	17.30	137.99	9.23	49.60	2013
352	0	2	15.3	7.36	137.81	24.70	49.29	2013
353	0	3	7.2	7.36	137.81	24.70	49.29	2013
355	0	1	11.7	13.70	138.33	27.68	48.85	2013
357	0	3	9	31.35	138.45	43.15	48.38	2013
358	0	3	18	22.22	138.30	14.90	49.33	2013
359	0	2	10.8	22.22	138.30	14.90	49.33	2013
360	0	3	20.7	22.22	138.30	14.90	49.33	2013
361	0	3	18.5	22.22	138.30	14.90	49.33	2013
362	0	2	17.4	22.22	138.30	14.90	49.33	2013
363	0	3	16.2	22.22	138.30	14.90	49.33	2013
365	0	3	15.3	19.23	138.23	9.23	49.38	2013
366	0	3	13.5	19.23	138.23	9.23	49.38	2013
367	0	2	8.1	8.10	137.61	10.98	49.95	2013
368	0	2	7.2	8.10	137.61	10.98	49.95	2013
369	0	1	5.4	7.98	137.49	5.40	48.80	2013
370	1	2	10.8	7.98	137.49	35.39	48.79	2013
371	1	3	7.2	26.32	132.31	13.06	49.84	2013
373	1	3	14.4	37.08	133.46	13.92	49.85	2013
374	0	2	12.6	43.03	134.13	45.04	46.99	2013
375	0	3	9	43.03	134.13	45.04	46.99	2013
376	1	2	9	39.03	132.81	13.06	49.68	2013
377	1	2	14.4	24.62	133.65	1.80	47.35	2013
378	1	2	16.2	24.62	133.65	1.80	47.35	2013
380	0	2	9	24.14	134.99	14.84	48.57	2013
381	0	2	11.7	42.87	135.21	15.12	48.10	2013
382	0	2	11.7	19.65	136.13	14.83	49.00	2013
386	0	2	15.3	41.57	137.96	33.75	48.90	2013
387	0	2	12.6	41.57	137.96	33.75	48.90	2013
388	0	2	9.9	48.63	138.00	40.84	48.70	2013

389	0	2	4.5	48.63	138.00	40.84	48.70	2013
390	0	2	13.5	39.44	134.92	43.35	47.92	2013
391	0	3	5.4	52.55	137.99	44.73	48.58	2013
392	0	2	7.2	65.95	137.77	46.56	47.64	2013
393	0	2	6.3	61.17	137.90	43.38	47.63	2013
394	0	2	9.9	73.00	137.43	48.88	47.93	2013
395	0	2	15.3	73.00	137.43	48.88	47.93	2013
396	0	3	5.4	73.00	137.43	48.88	47.93	2013
397	0	1	7.2	73.00	137.43	48.88	47.93	2013
398	0	1	8.1	73.00	137.43	48.88	47.93	2013
399	0	2	16.2	74.08	137.34	48.00	47.89	2013
400	0	1	10.8	60.65	136.47	31.15	47.93	2013
401	0	2	12.6	60.65	136.47	31.15	47.93	2013
402	0	1	5.4	69.84	135.33	42.15	47.32	2013
403	0	1	5.4	38.69	133.47	45.10	47.17	2013
404	0	1	8.1	38.69	133.47	45.10	47.17	2013
405	0	3	8.1	42.87	133.32	52.91	46.89	2013
406	0	2	25.2	43.21	135.37	46.35	48.42	2013
407	0	2	10.8	43.21	135.37	46.35	48.42	2013
408	0	2	9.9	32.24	132.73	81.32	45.39	2013
409	0	3	12.6	32.24	132.73	81.32	45.39	2013
412	0	2	18.9	23.30	131.36	62.79	44.80	2013
414	0	2	12.6	58.82	131.56	75.93	45.60	2013
417	0	2	7.2	58.82	131.56	75.93	45.60	2013
419	0	3	5.4	41.61	132.49	64.64	46.31	2013
420	0	3	10	41.61	132.49	64.64	46.31	2013
421	0	2	18	41.61	132.49	64.64	46.31	2013
422	0	1	10.8	41.61	132.49	64.64	46.31	2013
423	0	1	8.1	9.72	130.63	84.94	42.05	2013
424	0	2	16.2	9.72	130.63	84.94	42.05	2013
425	0	2	7.2	17.13	137.09	3.99	47.90	2013
427	0	2	16.2	27.41	132.44	66.89	46.65	2013
428	0	2	6.3	27.41	132.44	66.89	46.65	2013
429	0	1	9	27.41	132.44	66.89	46.65	2013
430	0	2	11.7	27.41	132.44	66.89	46.65	2013
431	0	2	11.7	26.97	133.58	55.37	47.23	2013
432	0	2	18	26.97	133.58	55.37	47.23	2013
433	0	3	14.4	26.97	133.58	55.37	47.23	2013
434	0	3	14.4	18.59	132.86	64.84	47.09	2013
435	0	3	7.2	18.59	132.86	64.84	47.09	2013
436	0	2	16.2	12.80	131.71	78.57	46.78	2013
438	0	2	10.8	12.80	131.71	78.57	46.78	2013
439	0	2	9	4.79	131.67	81.68	46.99	2013
440	0	1	9	4.79	131.67	81.68	46.99	2013
441	0	2	18	4.79	131.67	81.68	46.99	2013
443	0	2	6.3	20.53	133.47	64.57	47.81	2013

444	0	1	6.3	22.14	132.25	56.73	48.17	2013
445	0	3	6.8	22.14	132.25	56.73	48.17	2013
446	0	2	7.2	14.25	137.12	7.20	46.80	2013
447	0	2	13	14.25	137.12	1.40	46.80	2013
448	1	3	14.4	14.25	137.12	67.91	46.80	2013
449	0	2	19.8	6.29	130.26	69.34	47.65	2013
450	0	2	12.6	31.48	132.10	38.09	48.92	2013
451	0	3	5.4	17.13	131.15	47.22	48.45	2013
452	0	3	6.3	27.98	131.24	34.25	48.86	2013
453	0	3	10.8	27.98	131.24	34.25	48.86	2013
454	0	3	5.4	18.94	136.26	26.61	49.53	2013
455	0	3	12.6	18.94	136.26	26.61	49.53	2013
456	0	1	13.5	33.79	127.85	41.01	49.65	2013
457	0	2	19.8	33.79	127.85	41.01	49.65	2013
458	0	2	23.4	33.79	127.85	41.01	49.65	2013
459	0	2	10.8	25.61	128.86	30.23	49.82	2013
460	0	2	14.4	24.36	129.38	25.66	49.96	2013
461	0	2	10.8	24.36	129.38	25.66	49.96	2013
462	0	2	8.1	24.36	129.38	25.66	49.96	2013
464	0	2	8.1	24.09	126.63	53.76	49.40	2013
465	0	2	12.6	1.48	124.25	56.83	49.11	2013
466	0	3	14.4	9.47	123.39	51.85	48.77	2013
467	0	1	9	38.48	135.67	42.65	48.47	2013
468	0	2	8.5	38.48	135.67	42.65	48.47	2013
469	0	2	11.7	38.48	135.67	42.65	48.47	2013
470	0	2	9.9	15.47	122.19	43.15	48.47	2013
471	0	2	9	7.56	119.36	16.17	48.09	2013
472	0	2	15.3	7.56	119.36	16.17	48.09	2013
473	1	2	14.4	14.84	118.45	0.40	45.20	2013
474	1	2	14	14.84	118.45	0.40	45.20	2013
475	1	3	15	14.84	118.45	0.60	45.20	2013
476	0	1	13.5	22.40	119.06	9.23	48.50	2013
477	0	2	14.4	22.40	119.06	9.23	48.50	2013
478	0	2	6.3	36.27	117.22	22.14	48.22	2013
479	0	2	9	36.27	117.22	22.14	48.22	2013
480	0	1	10.8	56.55	114.55	29.10	47.52	2013
481	0	2	9	48.74	115.27	17.81	47.93	2013
483	0	3	12.6	38.05	133.10	39.40	48.79	2013
484	1	3	9.9	20.60	122.76	8.63	49.39	2013
485	1	2	13.5	13.06	121.91	8.63	49.23	2013
486	1	3	13.5	30.59	135.80	51.09	47.57	2013
487	1	3	20.7	24.32	133.23	0.90	48.27	2013
488	1	3	21.6	24.32	133.23	0.90	48.27	2013
489	1	3	18	46.49	130.92	26.77	48.86	2013
491	0	3	9	16.20	131.31	1.80	48.89	2013
492	1	3	10.8	16.20	131.31	44.75	48.88	2013

493	1	3	15.3	81.54	123.57	2.70	40.46	2013
494	0	3	8.1	81.54	123.57	4.50	40.47	2013
495	1	3	12.6	81.54	123.57	2.70	40.46	2013
496	1	2	23.4	6.96	134.53	9.00	48.49	2013
497	1	2	14.4	6.96	134.53	9.00	48.49	2013
499	1	2	16.2	66.28	123.72	16.49	41.22	2013
500	1	3	13.5	100.08	124.74	51.17	42.56	2013
504	1	2	18	12.58	134.93	0.09	49.97	2013
517	0	2	9	31.15	126.14	127.22	40.58	2013
518	0	1	6.3	31.15	126.14	127.22	40.58	2013
520	0	1	14.4	23.64	126.41	121.56	40.62	2013
521	0	1	12.6	49.16	124.76	143.75	40.20	2013
522	0	3	9.9	49.16	124.76	143.75	40.20	2013
523	0	3	8.1	7.59	131.97	81.19	42.64	2013
524	0	2	17.1	7.59	131.97	81.19	42.64	2013
526	0	3	5	60.84	122.76	158.50	39.51	2013
527	0	3	9	60.84	122.76	158.50	39.51	2013
529	0	1	16.2	96.78	117.77	202.15	37.90	2013
530	0	2	9.9	83.14	112.62	232.22	36.04	2013
531	0	2	10.8	79.66	112.98	228.79	36.16	2013
532	0	2	18	75.32	113.53	223.99	36.34	2013
534	0	2	9.9	70.73	114.29	217.96	36.59	2013
536	0	2	9	19.15	119.99	163.89	38.44	2013
537	0	3	2.7	19.15	119.99	163.89	38.44	2013
538	0	1	10.8	27.50	124.19	123.66	39.85	2013
539	0	2	15.3	37.33	125.44	110.23	40.30	2013
540	0	2	19.8	9.03	132.06	82.56	42.70	2013
541	0	2	15.3	32.05	125.39	114.16	40.24	2013
542	0	2	10.8	19.45	127.27	96.86	40.89	2013
543	0	3	12.6	19.45	127.27	96.86	40.89	2013
544	0	2	12.6	33.75	128.34	79.55	41.39	2013
546	0	2	11.7	53.56	116.97	181.46	37.55	2013
547	0	3	12.6	29.51	138.12	18.59	46.90	2013
548	0	1	9.9	37.87	137.70	19.24	46.72	2013
549	0	2	8.1	13.70	132.97	71.64	43.11	2013
550	0	2	16.2	13.70	132.97	71.64	43.11	2013
551	0	2	14.4	30.59	137.70	13.03	46.50	2013
552	0	1	6.3	155.55	104.99	243.59	33.60	2013
553	0	3	5.4	160.65	104.45	248.47	33.42	2013
555	0	1	7.2	168.87	103.53	260.66	33.12	2013
556	0	1	7.2	175.81	102.83	265.90	32.89	2013
557	0	1	7.8	175.81	102.83	265.90	32.89	2013
558	0	1	9	189.45	101.44	279.16	32.44	2013
559	0	2	2.5	189.45	101.44	279.16	32.44	2013
560	0	3	3.5	189.45	101.44	279.16	32.44	2013
561	0	3	7.2	199.98	100.44	282.95	32.12	2013

562	0	2	7.2	199.98	100.44	282.95	32.12	2013
564	0	1	10.8	199.98	100.44	282.95	32.12	2013
567	0	2	13.5	16.20	132.72	61.97	42.86	2013
568	0	3	4.5	215.91	99.03	282.68	31.67	2013
569	0	2	4.5	215.91	99.03	282.68	31.67	2013
570	0	1	15.3	214.36	99.43	266.34	31.82	2013
571	0	2	12.6	222.81	97.04	268.97	31.08	2013
572	0	3	7.2	222.81	97.04	268.97	31.08	2013
573	0	3	8.1	220.38	96.51	266.97	30.93	2013
574	0	1	14.4	220.38	96.51	266.97	30.93	2013
575	0	3	8.1	206.23	97.08	253.07	31.14	2013
576	0	1	7.2	193.71	96.41	240.98	30.98	2013
577	0	3	8.1	225.22	93.33	272.44	29.97	2013
581	0	2	5.4	11.71	131.99	59.81	42.59	2013
582	0	2	9	153.89	95.73	194.28	31.09	2013
584	0	1	9.9	161.77	94.88	201.14	30.84	2013
586	0	3	4.5	142.39	96.79	182.93	31.45	2013
587	0	2	7.2	142.39	96.79	182.93	31.45	2013
588	0	3	7.2	127.96	98.07	168.08	31.89	2013
589	0	1	3.6	127.96	98.07	168.08	31.89	2013
590	0	1	3.6	127.96	98.07	168.08	31.89	2013
591	0	3	10.8	149.32	106.44	190.41	34.17	2013
593	0	3	5.3	149.32	106.44	190.41	34.17	2013
595	0	3	7.2	132.40	109.33	170.38	35.13	2013
596	0	2	12.6	132.40	109.33	170.38	35.13	2013
597	0	1	9.9	132.40	109.33	170.38	35.13	2013
598	0	3	5.4	102.48	114.76	127.15	37.05	2013
599	0	2	10.8	102.48	114.76	127.15	37.05	2013
600	0	2	10.8	102.48	114.76	127.15	37.05	2013
601	0	2	11	102.48	114.76	127.15	37.05	2013
602	0	2	12.6	5.77	134.69	53.96	43.78	2013
603	0	2	15.3	5.77	134.69	53.96	43.78	2013
604	0	1	5.4	10.96	110.18	42.61	36.10	2013
604	0	1	7.2	10.96	110.18	42.61	36.10	2013
605	0	1	3.6	14.37	109.97	42.37	36.05	2013
605	0	1	8.1	14.37	109.97	42.37	36.05	2013
607	0	2	6.3	20.42	111.78	20.42	36.76	2013
608	0	1	8.4	20.42	111.78	20.42	36.76	2013
609	0	1	8.1	83.78	117.19	139.65	37.81	2013
610	0	2	7.2	83.78	117.19	139.65	37.81	2013
611	0	2	14.4	83.78	117.19	139.65	37.81	2013
612	0	1	11.7	59.58	121.32	140.79	39.15	2013
613	0	1	9.9	55.58	122.01	134.44	39.36	2013
614	0	3	7.2	55.58	122.01	134.44	39.36	2013
615	0	2	12.6	43.82	127.59	78.06	41.63	2013
616	0	3	9	43.82	127.59	78.06	41.63	2013

618	0	1	9.9	44.50	133.23	20.90	44.04	2013
619	0	2	10.8	2.70	128.62	92.00	41.30	2013
621	0	2	19.8	0.90	135.94	33.44	44.39	2013
622	0	1	17.8	0.90	135.94	33.44	44.39	2013
628	0	2	10.8	1.00	134.41	58.40	43.59	2013
629	0	1	10.3	0.50	134.41	58.40	43.59	2013
630	0	1	19.8	7.59	134.41	58.40	43.59	2013
631	0	2	22.5	7.59	134.41	58.40	43.59	2013
632	0	1	13.5	0.90	137.24	9.47	45.45	2013
633	0	1	19.8	5.40	137.24	9.47	45.45	2013
637	0	2	23.4	6.90	137.75	26.06	48.63	2013
638	0	2	8.1	8.10	137.75	26.06	48.63	2013
639	0	2	14.4	1.80	137.75	26.06	48.63	2013
640	0	3	7.2	1.80	134.22	60.11	43.55	2013
642	0	1	5.4	3.60	128.50	98.60	41.26	2013
643	0	2	16	2.50	137.04	14.37	45.58	2013
646	0	1	10.8	2.70	136.47	27.84	45.52	2013
647	0	1	19.8	6.30	136.47	27.84	45.52	2013
652	0	2	15.3	4.50	137.88	17.77	48.23	2013
653	0	2	4.5	7.20	138.08	26.77	49.02	2013
654	0	1	9	2.70	138.08	26.77	49.02	2013
656	0	2	23.4	10.80	135.71	12.58	50.02	2013
658	0	2	16.2	2.70	135.72	9.03	49.38	2013
659	0	3	19.8	6.30	135.72	9.03	49.37	2013
660	1	2	30.6	12.70	135.72	9.03	49.36	2013
662	0	1	9	7.20	134.03	14.37	50.16	2013
663	0	3	5.4	10.80	134.03	14.37	50.16	2013
664	0	2	16.2	1.00	134.03	14.37	50.16	2013
665	0	2	10.8	1.00	130.06	78.74	41.81	2013
667	0	2	17.1	8.10	133.77	19.95	50.83	2013
669	0	2	16.2	0.09	137.86	33.88	47.27	2013
671	0	2	8.1	0.09	137.86	33.88	47.27	2013
673	0	1	23.4	9.00	137.54	26.52	49.52	2013
674	0	1	14	0.40	137.54	26.52	49.52	2013
678	0	3	23.4	0.90	122.97	6.96	50.76	2013
679	0	2	16.2	3.60	122.97	6.96	50.76	2013
680	0	3	16	3.80	122.97	6.96	50.76	2013
683	0	2	18	3.60	121.04	13.06	50.15	2013
684	0	2	19.8	5.40	121.04	13.06	50.15	2013
685	0	2	22.5	8.10	121.04	13.06	50.15	2013
688	0	2	21.6	0.80	129.95	42.75	48.48	2013
689	0	3	15.3	1.80	129.95	42.75	48.48	2013
693	0	1	9.9	3.10	127.57	79.27	46.78	2013
694	0	2	13	1.00	127.57	79.27	46.78	2013
695	0	3	19.8	6.80	127.57	79.27	46.78	2013
696	0	3	13.5	0.50	127.57	79.27	46.78	2013

698	0	2	9	2.60	129.38	91.23	41.57	2013
699	0	3	16.2	8.10	129.38	91.23	41.57	2013
700	0	2	7.2	9.00	132.07	32.17	48.31	2013
701	0	2	13.5	2.70	132.07	32.17	48.31	2013
702	0	2	18	0.09	130.62	71.64	46.67	2013
704	0	1	11.7	2.70	113.31	8.10	36.41	2013
705	1	2	19.8	1.30	113.31	134.85	36.40	2013
707	0	1	18	37.76	130.47	93.70	42.39	2013
708	0	3	10.8	0.09	120.37	41.72	49.51	2013
710	0	3	10.8	0.13	124.24	57.16	49.07	2013
711	0	1	13.5	0.13	124.24	57.16	49.07	2013
713	0	2	9	1.80	131.90	80.78	47.17	2013
714	0	3	4.5	6.30	131.90	80.78	47.17	2013
715	0	3	10.8	2.70	129.97	61.40	47.86	2013
717	0	2	8	3.00	130.28	78.71	41.89	2013
721	0	1	16.3	1.00	134.81	13.76	49.95	2013
722	0	3	18	1.00	134.81	13.76	49.95	2013
723	0	2	25	7.00	134.81	13.76	49.95	2013
724	0	2	10.8	3.60	134.81	13.76	49.95	2013
726	0	3	9	3.60	135.38	24.80	49.27	2013
727	0	1	21.6	1.00	135.77	2.10	48.93	2013
728	0	1	22.6	1.00	135.77	3.10	48.93	2013
729	0	3	11.7	3.60	135.77	7.80	48.94	2013
730	0	1	14.4	5.40	135.77	5.10	48.94	2013
731	0	2	14.4	5.40	135.77	5.10	48.94	2013
732	0	1	15.4	4.40	135.77	4.10	48.93	2013
733	1	3	19.5	0.30	135.77	1.00	48.93	2013
737	0	1	13.4	0.30	137.71	18.55	50.08	2013
738	0	2	9	10.80	137.71	18.94	50.00	2013
739	0	3	9	10.80	137.71	18.94	50.00	2013
740	0	1	19.8	0.90	137.71	18.94	50.00	2013
743	0	2	13.5	2.70	112.87	25.11	37.48	2013
745	0	1	12.5	0.10	131.06	71.30	42.19	2013
746	0	1	19.8	7.20	131.06	71.30	42.19	2013
747	0	1	18	7.20	127.16	36.97	51.27	2013
748	0	1	12.6	1.80	127.16	36.97	51.27	2013
750	0	3	12.6	2.70	130.17	16.20	49.45	2013
751	0	3	16.2	6.30	130.17	16.20	49.45	2013
752	0	1	9	0.90	130.17	16.20	49.45	2013
753	0	3	17.1	7.20	130.17	16.20	49.45	2013
754	0	2	9	3.60	118.55	14.84	47.85	2013
755	0	3	14.4	2.94	137.94	11.71	49.90	2013
756	0	3	17.1	0.90	137.94	11.71	49.90	2013
757	0	3	16	2.00	137.94	11.71	49.90	2013
760	0	3	5.7	4.73	130.06	65.04	47.76	2013
761	0	3	13.5	2.70	130.06	65.04	47.76	2013

766	0	2	9.9	2.70	135.17	48.27	44.00	2013
767	0	3	10.8	3.60	137.57	7.41	45.98	2013
769	0	2	18	1.00	126.13	74.11	41.66	2013
770	0	3	16	0.20	134.28	6.96	50.61	2013
771	0	1	17.5	0.40	124.51	26.51	50.86	2013
773	0	2	12.6	4.50	124.51	26.51	50.86	2013
774	0	2	12.8	4.30	124.51	26.51	50.86	2013
775	0	2	12.6	4.50	127.18	23.96	51.23	2013
777	0	1	30.6	13.03	127.18	23.96	51.23	2013
778	0	1	12.6	1.00	136.05	36.98	44.43	2013
779	0	2	21.6	1.80	136.05	36.98	44.43	2013
780	0	1	10	7.56	125.01	70.19	48.27	2013
781	0	2	15.8	2.20	125.01	70.19	48.27	2013
782	0	2	18	7.20	122.93	43.85	50.00	2013
783	0	2	19.8	5.40	122.93	43.85	50.00	2013
784	0	2	23.4	1.80	122.93	43.85	50.00	2013
785	0	3	30	4.80	122.93	43.85	50.00	2013
787	0	1	14.4	7.20	130.65	3.99	51.03	2013
788	0	2	18	3.60	130.65	3.99	51.03	2013
789	0	1	11.7	9.90	130.65	3.99	51.03	2013
793	0	2	21.5	10.80	130.61	26.32	50.97	2013
795	0	2	28	6.40	137.08	31.81	45.45	2013
796	0	2	29	7.40	137.08	31.81	45.45	2013
797	0	1	14.7	1.50	137.08	31.81	45.45	2013
798	0	1	27	5.40	137.08	31.81	45.45	2013
799	0	1	25.2	3.60	137.08	31.81	45.45	2013
800	0	1	27.9	6.30	137.08	31.81	45.45	2013
2	0	1	9	4.42	252.51	96.83	7.48	2017
4	0	2	9	12.58	250.86	120.57	7.57	2017
5	0	3	5.4	12.58	250.86	120.57	7.57	2017
6	0	3	9.9	17.67	255.97	84.04	7.71	2017
8	0	3	15.3	1.00	211.03	121.55	6.39	2017
9	0	2	5.4	1.00	211.03	121.55	6.39	2017
11	0	2	12.6	9.38	213.51	112.17	6.45	2017
12	0	2	12.6	18.72	218.18	107.50	6.57	2017
13	0	1	14.4	7.98	256.42	70.44	7.54	2017
14	0	3	4.5	7.98	256.42	70.44	7.54	2017
15	0	2	4.5	7.98	256.42	70.44	7.54	2017
16	0	2	7.2	16.36	216.82	123.21	6.52	2017
18	0	1	7.2	41.51	221.53	71.26	6.72	2017
19	0	2	10.8	41.51	221.53	71.26	6.72	2017
21	0	2	14.4	64.37	219.33	64.37	6.73	2017
22	0	2	5.4	37.75	224.11	37.75	6.89	2017
23	0	2	7.2	26.61	226.34	26.61	6.96	2017
24	0	2	7.2	26.61	226.34	26.61	6.96	2017
26	0	3	19.8	43.12	228.30	29.88	6.98	2017

27	0	2	6.3	31.15	236.46	32.40	7.24	2017
28	0	1	6.3	31.15	236.46	32.40	7.24	2017
29	0	1	9	1.00	256.16	63.05	7.56	2017
30	0	2	30.6	1.00	256.16	63.05	7.56	2017
31	0	1	5.4	1.00	257.16	63.05	7.56	2017
32	0	1	6.5	30.98	236.77	32.45	7.25	2017
33	0	2	9	32.94	241.39	41.72	7.44	2017
34	0	1	9	32.94	241.39	41.72	7.44	2017
36	0	1	4.5	1.00	235.09	3.99	7.23	2017
37	1	2	10.8	3.99	234.38	18.88	7.21	2017
38	0	1	4.5	7.36	234.51	6.96	7.22	2017
39	0	1	4.5	16.74	237.81	20.60	7.33	2017
40	0	2	9	28.76	231.07	19.17	7.08	2017
41	0	2	15.3	28.76	231.07	19.17	7.08	2017
42	0	1	6.3	28.76	231.07	19.17	7.08	2017
44	0	2	22.5	1.00	258.83	48.24	7.62	2017
48	0	2	5.4	79.82	228.45	79.82	7.13	2017
49	0	1	5.4	79.82	228.45	79.82	7.13	2017
54	0	2	9	37.79	241.15	110.62	7.54	2017
56	0	3	11.7	23.34	232.33	150.30	7.30	2017
57	0	1	10.8	34.25	231.95	148.17	7.29	2017
60	0	1	6.3	44.80	234.41	132.88	7.35	2017
62	0	1	12.6	53.53	232.77	141.42	7.30	2017
63	0	1	10.8	56.54	231.95	145.90	7.27	2017
64	0	1	16.2	55.09	231.74	147.20	7.24	2017
66	0	1	16.8	39.04	235.22	127.14	7.27	2017
67	0	2	18.8	43.38	235.06	128.18	7.24	2017
68	0	1	10.8	48.43	235.16	128.25	7.22	2017
69	0	1	13.5	48.43	235.16	128.25	7.22	2017
70	0	2	8.1	34.60	237.32	116.36	7.30	2017
71	0	2	11.7	34.60	237.32	116.36	7.30	2017
72	0	3	11.7	34.60	237.32	116.36	7.30	2017
73	0	2	12.6	18.59	259.16	50.56	7.73	2017
74	0	1	7.2	18.59	259.16	50.56	7.73	2017
75	0	1	9.9	18.59	259.16	50.56	7.73	2017
77	0	1	10.7	18.59	259.16	50.56	7.73	2017
78	0	2	16.2	18.59	259.16	50.56	7.73	2017
81	0	2	4.5	52.08	231.88	144.85	7.21	2017
82	0	3	12.6	52.08	231.88	144.85	7.21	2017
83	0	1	17.1	52.08	231.88	144.85	7.21	2017
84	0	2	12.6	52.08	231.88	144.85	7.21	2017
85	0	3	13.5	52.08	231.88	144.85	7.21	2017
86	0	1	9	52.78	231.84	145.73	7.23	2017
87	0	2	14.4	52.78	231.84	145.73	7.23	2017
88	0	2	14.9	52.78	231.84	145.73	7.23	2017
92	0	2	16.2	11.84	241.78	92.37	7.58	2017

97	0	2	21.6	1.00	242.38	92.51	7.56	2017
98	0	1	11.7	16.57	243.49	99.03	7.61	2017
99	0	2	8.1	16.57	243.49	99.03	7.61	2017
100	0	2	8.5	16.57	243.49	99.03	7.61	2017
101	0	2	20.7	1.00	248.81	67.80	7.76	2017
102	0	2	18	21.67	241.77	93.98	7.51	2017
103	0	2	13.5	12.70	249.16	50.30	7.60	2017
105	0	2	18	14.92	248.80	52.08	7.58	2017
107	0	2	14.4	40.08	244.47	79.45	7.45	2017
108	0	3	16.2	39.36	245.50	74.07	6.48	2017
109	0	3	7.2	39.36	245.50	74.07	7.48	2017
110	0	1	12.6	4.42	259.58	4.79	7.33	2017
111	0	1	13	0.13	260.58	4.79	7.33	2017
112	0	2	16.2	0.13	260.58	4.79	7.33	2017
113	0	3	9.9	0.13	260.58	4.79	7.33	2017
116	1	3	12.6	1.86	259.61	10.31	7.34	2017
118	0	2	18.9	1.00	260.61	1.00	7.34	2017
120	0	3	17.1	8.24	263.08	54.70	7.51	2017
121	0	2	13.5	8.24	263.08	54.70	7.51	2017
124	0	2	27	1.00	263.39	55.03	7.55	2017
125	0	1	5.4	9.72	263.12	49.59	7.52	2017
127	0	2	9	60.38	248.55	114.07	7.25	2017
128	0	3	16.2	5.77	263.43	49.45	7.55	2017
132	0	2	6.3	1.00	263.39	24.32	7.60	2017
135	0	2	11.7	34.42	242.18	72.19	7.16	2017
136	0	1	12.6	34.42	242.18	72.19	7.16	2017
138	0	1	16.2	34.42	242.18	72.19	7.16	2017
141	0	2	15.3	40.77	238.08	77.59	6.87	2017
142	0	1	21.6	40.77	238.08	77.59	6.87	2017
143	0	1	9.9	40.77	238.08	77.59	6.87	2017
144	0	2	21.6	40.77	238.08	77.59	6.87	2017
146	0	2	17.1	40.58	231.17	134.22	6.94	2017
147	0	2	12.6	40.58	231.17	134.22	6.94	2017
148	0	3	15.3	61.16	232.50	121.56	6.85	2017
149	0	2	6.3	32.17	253.97	80.52	7.38	2017
150	0	3	15.3	32.17	253.97	80.52	7.38	2017
151	0	3	7.2	20.90	229.30	60.75	6.48	2017
153	0	2	16.2	20.90	229.30	60.75	6.48	2017
154	0	2	14.4	20.90	229.30	60.75	6.48	2017
155	0	3	10.8	29.03	230.33	58.18	6.52	2017
156	0	3	14.4	40.08	231.30	58.18	6.57	2017
157	0	2	6.3	25.19	233.81	37.04	6.59	2017
159	0	2	2.7	1.00	239.65	7.59	6.73	2017
161	0	2	9.9	1.00	239.65	7.59	6.73	2017
162	0	2	14.4	1.00	239.65	7.59	6.73	2017
163	0	1	15	1.00	239.65	7.59	6.73	2017

166	0	2	13.8	1.00	240.83	1.00	6.76	2017
167	1	2	18	1.00	240.83	1.00	6.76	2017
169	0	2	29.5	1.00	240.83	1.00	6.76	2017
170	0	3	9.9	7.10	242.10	7.10	6.80	2017
172	0	2	15	6.96	244.18	25.99	6.89	2017
174	0	2	25.2	1.00	243.95	21.35	6.83	2017
175	0	1	30.6	1.00	243.95	21.35	6.83	2017
176	0	2	4.5	1.00	243.95	21.35	6.83	2017
178	0	2	12.6	39.81	252.16	92.96	7.37	2017
180	0	2	19.8	1.00	246.24	34.30	6.89	2017
182	0	3	22	1.00	246.24	34.30	6.89	2017
183	0	2	26.1	1.00	246.24	34.30	6.89	2017
184	0	3	6.3	1.00	246.24	34.30	6.89	2017
187	0	2	9.9	4.79	246.90	39.08	6.90	2017
191	0	1	9	34.94	234.08	119.75	7.34	2017
193	1	3	16.3	1.00	251.59	1.00	7.15	2017
194	0	1	9.9	1.00	251.59	1.00	7.15	2017
195	0	2	22.5	1.00	251.29	15.19	7.06	2017
197	0	2	8.1	1.00	251.93	9.23	7.08	2017
202	0	3	20.7	1.00	245.19	150.07	7.30	2017
204	0	1	17.1	13.50	260.94	23.72	7.61	2017
206	1	2	23.4	9.23	254.00	1.00	7.11	2017
209	0	2	16.2	1.00	254.91	13.38	7.12	2017
214	0	3	9	1.00	256.41	21.96	7.17	2017
215	0	2	10.8	3.99	256.19	18.94	7.17	2017
218	0	1	13.5	4.73	255.89	26.65	7.19	2017
220	0	2	18	1.00	256.89	26.65	7.19	2017
221	0	2	13.5	1.00	256.89	26.65	7.19	2017
222	0	2	4.5	1.00	256.89	26.65	7.19	2017
223	0	1	10.8	1.00	257.10	27.51	7.21	2017
225	0	2	11.7	1.00	257.10	27.51	7.21	2017
226	0	1	10.8	34.08	257.63	43.35	7.32	2017
228	0	1	12.6	12.82	260.31	33.28	7.57	2017
230	0	2	23.4	1.00	248.80	35.24	6.95	2017
231	0	2	10.8	1.00	249.80	35.24	6.95	2017
232	0	3	13.5	5.77	247.65	45.60	6.90	2017
233	0	3	9	5.77	247.65	45.60	6.90	2017
234	0	3	14.4	13.92	246.56	46.25	6.87	2017
235	0	3	9	13.92	246.56	46.25	6.87	2017
237	0	1	9	0.13	243.63	32.45	6.83	2017
239	0	1	4.5	0.13	244.63	32.45	6.83	2017
240	0	3	5.4	9.23	241.44	13.03	6.75	2017
241	0	2	23.4	9.23	241.44	13.03	6.75	2017
242	0	3	12.6	9.23	241.44	13.03	6.75	2017
243	0	3	7.2	9.03	238.81	11.96	6.71	2017
245	0	1	25.2	1.00	239.81	11.96	6.71	2017

246	0	2	27	1.00	237.48	13.70	6.68	2017
252	0	2	12.6	1.00	249.60	75.12	6.89	2017
253	0	1	23.4	1.00	249.60	75.12	6.89	2017
254	0	2	8.1	1.00	249.60	75.12	6.89	2017
256	0	3	3.5	3.48	248.52	85.55	6.85	2017
257	0	2	5.5	3.48	248.52	85.55	6.85	2017
258	0	2	9	9.47	248.59	75.07	6.86	2017
259	0	2	16.2	9.47	248.59	75.07	6.86	2017
260	0	2	16.2	9.47	248.59	75.07	6.86	2017
261	0	3	3.6	9.47	248.59	75.07	6.86	2017
262	0	1	12.6	9.47	248.59	75.07	6.86	2017
266	0	2	8.1	22.84	243.55	90.72	6.74	2017
267	0	1	16.2	43.65	231.71	119.16	7.26	2017
269	0	2	7.2	15.47	248.76	53.64	6.89	2017
270	0	1	9	19.50	243.20	89.47	6.74	2017
271	0	2	2.7	19.50	243.20	89.47	6.74	2017
272	0	2	7	14.84	242.83	89.72	5.73	2017
274	0	2	10.8	1.00	229.28	58.69	6.45	2017
275	0	2	14.4	1.00	229.28	58.69	6.45	2017
277	0	2	9.9	46.14	219.71	46.14	6.10	2017
278	0	3	9	46.14	219.71	46.14	6.10	2017
279	0	3	12.6	48.63	219.24	48.63	6.09	2017
282	0	3	4.5	1.00	229.37	60.35	6.32	2017
284	0	1	7.2	12.35	230.77	39.00	6.37	2017
286	0	2	16.2	12.35	230.77	39.00	6.37	2017
287	0	3	2.7	12.35	230.77	39.00	6.37	2017
288	0	3	25.2	1.00	230.23	17.77	6.40	2017
291	1	3	16.2	1.00	228.39	1.00	6.36	2017
292	0	2	27	1.00	229.39	1.00	6.36	2017
294	0	2	16.2	18.77	225.61	18.77	6.26	2017
295	0	1	22.5	18.77	225.61	18.77	6.26	2017
296	0	2	27	18.77	225.61	18.77	6.26	2017
297	0	1	13.5	32.97	223.69	32.97	6.23	2017
298	0	1	12.6	32.97	223.69	32.97	6.23	2017
299	0	1	12.6	36.97	223.21	36.97	6.22	2017
300	0	3	19.8	36.97	223.21	36.97	6.22	2017
301	0	1	4	26.11	234.13	39.61	6.55	2017
302	0	2	5.4	28.50	232.71	28.50	6.48	2017
303	0	3	13.5	1.00	256.81	66.41	7.44	2017
304	0	1	4	32.35	234.12	32.35	6.52	2017
305	0	1	5.4	24.49	234.05	24.49	6.50	2017
306	0	2	7.2	24.49	234.05	24.49	6.50	2017
310	0	1	4	7.98	232.35	17.40	6.44	2017
311	0	2	5.4	7.98	232.35	17.40	6.44	2017
314	0	3	23.4	1.00	231.11	50.21	6.40	2017
319	0	2	10.8	10.98	234.16	56.24	6.46	2017

320	0	3	6.3	10.98	234.16	56.24	6.46	2017
321	0	2	20.7	13.86	234.33	60.64	6.46	2017
322	0	1	9.9	13.86	234.33	60.64	6.46	2017
323	0	1	11.7	13.86	234.33	60.64	6.46	2017
325	0	1	17.1	1.00	236.04	68.81	6.54	2017
326	0	1	13.5	1.00	237.04	68.81	6.54	2017
327	0	2	12.6	13.92	255.22	78.14	7.37	2017
330	0	1	4.5	13.92	255.22	78.14	7.37	2017
332	0	2	23.4	11.22	237.63	59.58	6.57	2017
334	0	2	18	1.00	239.58	63.64	6.63	2017
335	0	1	13.5	1.00	239.58	63.64	6.63	2017
336	0	2	15.3	1.00	239.58	63.64	6.63	2017
337	0	2	27	26.21	261.35	50.20	7.52	2017
338	0	3	6.3	26.21	261.35	50.20	7.52	2017
339	0	1	16.2	26.98	260.91	57.39	7.53	2017
340	0	1	16.2	36.54	259.61	44.98	7.57	2017
350	0	3	10.8	1.00	259.37	45.80	7.51	2017
352	0	2	15.3	7.36	262.58	34.75	7.60	2017
354	0	1	14.4	1.00	263.58	34.75	7.60	2017
355	0	1	11.7	13.70	263.29	26.51	7.67	2017
356	0	2	5.4	13.70	263.29	26.51	7.67	2017
357	0	3	9	20.95	262.59	30.43	7.72	2017
358	0	3	18	22.22	262.97	50.11	7.69	2017
359	0	2	10.8	22.22	262.97	50.11	7.69	2017
360	0	3	20.7	22.22	262.97	50.11	7.69	2017
362	0	2	17.4	22.22	262.97	50.11	7.69	2017
364	0	3	6.3	22.22	262.97	50.11	7.69	2017
367	0	2	8.1	8.10	261.88	54.62	7.67	2017
368	0	2	7.2	8.10	261.88	54.62	7.67	2017
371	0	3	7.2	26.32	255.20	26.32	7.46	2017
372	0	2	3.6	26.32	255.20	26.32	7.46	2017
373	0	3	14.4	37.08	256.89	37.08	7.50	2017
376	0	2	9	39.03	255.36	39.03	7.51	2017
379	0	2	17.1	24.61	253.90	24.61	7.68	2017
380	0	2	9	24.14	255.15	24.14	7.77	2017
381	0	2	11.7	42.87	255.07	42.87	7.80	2017
382	0	2	11.7	19.65	257.56	19.65	7.76	2017
383	0	1	13.5	19.65	257.56	19.65	7.76	2017
384	0	1	12.6	39.36	261.76	63.16	7.74	2017
385	0	3	8.1	39.36	261.76	63.16	7.74	2017
386	0	2	15.3	41.57	261.18	60.64	7.76	2017
387	0	2	12.6	41.57	261.18	60.64	7.76	2017
388	0	2	9.9	48.63	261.09	64.34	7.77	2017
389	0	2	4.5	48.63	261.09	64.34	7.77	2017
390	0	3	13.5	22.22	260.19	53.54	7.44	2017
394	0	2	9.9	60.50	259.11	71.46	7.80	2017

395	0	2	15.3	60.50	259.11	71.46	7.80	2017
397	0	1	7.2	60.50	259.11	71.46	7.80	2017
398	0	1	8.1	60.50	259.11	71.46	7.80	2017
399	0	2	16.2	61.81	258.88	73.55	7.80	2017
400	0	1	10.8	57.74	257.19	60.65	7.81	2017
401	0	2	12.6	57.74	257.19	60.65	7.81	2017
402	0	1	5.4	40.79	254.61	72.51	7.80	2017
403	0	1	5.4	27.09	251.30	68.59	7.79	2017
404	0	1	8.1	27.09	251.30	68.59	7.79	2017
410	0	2	3.6	25.43	249.80	92.74	7.65	2017
411	0	1	16.2	26.52	247.12	76.02	7.61	2017
412	0	3	18.9	23.30	245.69	66.77	7.57	2017
413	0	1	9	9.38	242.64	161.14	7.21	2017
415	0	2	16.2	1.00	253.15	93.56	7.26	2017
416	0	2	17.1	1.00	253.15	93.56	7.26	2017
417	0	2	7.2	1.00	253.15	93.56	7.26	2017
418	0	2	9.9	14.25	255.44	81.45	7.32	2017
422	0	1	10.8	14.25	255.44	81.45	7.32	2017
423	0	1	8.1	15.12	243.62	155.61	7.24	2017
425	0	3	7.2	12.89	261.98	17.13	7.58	2017
426	0	2	11.7	1.00	255.01	82.28	7.30	2017
437	0	2	9.3	1.00	255.37	92.37	7.24	2017
438	0	2	10.8	1.00	255.37	92.37	7.24	2017
440	0	1	9	1.00	255.62	94.34	7.23	2017
442	0	1	5.4	1.00	255.62	94.34	7.23	2017
443	0	2	6.3	1.00	258.63	75.30	7.34	2017
446	0	2	7.2	10.39	261.86	17.77	7.59	2017
447	0	2	13	10.39	261.86	17.77	7.59	2017
448	0	3	14.4	10.39	261.86	17.77	7.59	2017
455	0	3	12.6	1.00	262.77	54.90	7.48	2017
456	0	1	13.5	11.22	253.39	71.87	7.01	2017
458	0	2	23.4	11.22	253.39	71.87	7.01	2017
463	0	2	18	1.00	251.54	73.23	6.95	2017
464	0	2	8.1	6.18	251.58	78.07	6.94	2017
469	0	2	11.7	31.15	261.46	47.34	7.47	2017
472	0	2	15.3	1.00	239.96	121.01	6.60	2017
474	0	2	14	1.00	238.63	116.33	6.56	2017
475	0	3	15	1.00	238.63	116.33	6.56	2017
480	0	1	10.8	1.00	231.82	85.92	6.38	2017
481	0	3	9	11.53	233.24	76.60	6.42	2017
482	0	1	3.6	11.53	233.24	76.60	6.42	2017
490	0	3	21.6	34.33	251.80	34.33	7.59	2017
494	1	3	8.1	1.00	230.97	1.00	7.12	2017
495	1	3	12.6	1.00	230.97	1.00	7.12	2017
496	0	2	23.4	1.00	261.54	12.58	7.38	2017
498	0	3	9.9	1.00	261.54	12.58	7.38	2017

499	1	3	16.2	16.49	231.02	16.49	7.10	2017
500	0	3	13.5	51.17	233.86	51.17	7.27	2017
501	0	3	12.6	34.40	224.20	34.68	6.20	2017
502	0	1	5.4	62.32	234.09	66.83	7.29	2017
503	0	2	4.5	12.11	238.31	105.62	7.20	2017
504	0	2	18	12.58	261.80	31.16	7.39	2017
505	0	2	3.6	12.58	261.80	31.16	7.39	2017
506	0	2	10.8	12.58	261.80	31.16	7.39	2017
507	0	1	14.4	20.11	246.96	31.72	7.00	2017
508	0	1	9	7.35	246.42	39.23	6.88	2017
509	0	1	5.4	12.74	248.00	42.79	6.92	2017
510	0	3	6.3	8.46	241.62	75.57	6.69	2017
511	0	3	3.6	24.26	259.70	43.02	7.28	2017
512	0	2	2.7	24.53	258.91	57.93	7.43	2017
513	0	3	4.5	24.53	258.91	57.93	7.43	2017
514	0	2	7.2	30.49	255.47	69.90	7.44	2017
515	0	2	4.5	51.39	229.45	216.93	6.80	2017
516	0	2	7.2	51.39	229.45	216.93	6.80	2017
518	0	1	6.3	31.15	235.86	192.06	6.97	2017
519	0	2	9	13.68	259.56	45.65	7.75	2017
523	0	3	8.1	3.99	246.54	138.37	7.32	2017
524	0	3	17.1	3.99	246.54	138.37	7.32	2017
525	0	2	9.9	3.99	246.54	138.37	7.32	2017
527	0	3	9	60.84	230.01	219.71	6.77	2017
528	0	3	11.7	27.50	234.15	205.15	6.94	2017
529	0	2	16.2	103.58	221.13	263.66	6.48	2017
530	0	2	9.9	67.29	211.13	291.47	6.21	2017
531	0	2	10.8	64.16	211.76	288.12	6.23	2017
532	0	2	18	62.38	212.77	285.21	6.26	2017
533	0	3	18.9	62.38	212.77	285.21	6.26	2017
535	0	1	5.4	62.95	214.16	282.94	6.30	2017
536	0	2	9	43.93	224.19	233.62	6.63	2017
537	0	3	2.7	43.93	224.19	233.62	6.63	2017
540	0	3	19.8	9.03	245.83	136.16	6.33	2017
542	0	2	10.8	19.45	237.01	184.69	7.05	2017
544	0	2	12.6	33.75	238.85	161.22	7.14	2017
545	0	3	18	8.10	220.02	208.74	6.53	2017
548	0	1	9.9	28.99	258.75	58.10	7.76	2017
549	0	2	8.1	11.96	248.78	124.55	7.37	2017
549	0	3	6.3	11.96	248.78	124.55	7.37	2017
550	0	2	16.2	11.96	248.78	124.55	7.37	2017
551	0	2	14.4	27.50	258.59	58.70	7.75	2017
552	0	1	6.3	39.30	197.13	321.68	5.79	2017
554	0	2	14.4	33.56	196.16	327.36	5.76	2017
555	0	1	7.2	21.96	194.53	339.42	5.71	2017
556	0	1	7.2	14.99	193.27	346.03	5.67	2017

557	0	1	7.8	14.99	193.27	346.03	5.67	2017
559	0	2	2.5	1.00	190.78	360.88	5.59	2017
560	0	3	3.5	1.00	190.78	360.88	5.59	2017
561	0	3	7.2	11.22	187.94	367.91	5.54	2017
562	0	2	7.2	1.00	188.94	367.91	5.54	2017
563	0	2	10.8	1.00	188.94	367.91	5.54	2017
565	0	3	23.4	25.65	190.20	350.06	5.58	2017
566	0	2	7	25.65	190.20	350.06	5.58	2017
567	0	2	13.5	13.30	247.43	137.04	7.36	2017
568	0	3	4.5	21.22	186.28	374.25	5.46	2017
569	0	2	4.5	21.22	186.28	374.25	5.46	2017
570	0	1	15.3	36.06	186.96	362.10	5.49	2017
574	0	1	14.4	81.57	181.51	375.64	5.33	2017
577	0	3	8.1	130.26	175.61	392.59	5.16	2017
578	0	1	11.8	130.26	175.61	392.59	5.16	2017
579	0	2	12.6	98.33	181.73	350.84	5.35	2017
580	0	3	13	102.98	181.84	352.02	5.36	2017
583	0	2	5.4	10.27	180.09	328.39	5.33	2017
585	0	3	4.5	1.00	177.57	335.60	5.28	2017
586	0	3	4.5	20.44	181.00	316.94	5.39	2017
587	0	2	7.2	1.00	182.00	316.94	5.39	2017
589	0	1	3.6	14.92	184.23	302.21	5.46	2017
590	0	1	3.6	14.92	184.23	302.21	5.46	2017
591	0	3	10.8	89.07	199.53	281.36	5.89	2017
592	0	1	10	89.07	199.53	281.36	5.89	2017
593	0	3	5.3	89.07	199.53	281.36	5.89	2017
594	0	1	10.8	76.93	204.72	253.96	6.05	2017
596	0	2	12.6	76.93	204.72	253.96	6.05	2017
597	0	1	9.9	76.93	204.72	253.96	6.05	2017
599	0	2	10.8	26.61	214.34	194.42	6.37	2017
600	0	2	10.8	26.61	214.34	194.42	6.37	2017
601	0	2	11	26.61	214.34	194.42	6.37	2017
604	0	1	7.2	42.54	205.61	174.95	6.15	2017
605	0	1	3.6	40.80	205.23	175.65	6.14	2017
605	0	1	8.1	40.80	205.23	175.65	6.14	2017
606	0	2	10.8	20.42	208.46	154.26	6.25	2017
608	0	1	8.4	20.42	208.46	154.26	6.25	2017
611	0	2	14.4	1.00	218.79	186.65	6.51	2017
613	0	1	9.9	7.56	227.42	166.74	6.79	2017
614	0	3	7.2	7.56	227.42	166.74	6.79	2017
615	0	2	12.6	64.99	237.40	113.46	7.16	2017
616	0	3	9	64.99	237.40	113.46	7.16	2017
617	0	1	19.8	9.58	248.38	110.12	6.56	2017
619	0	2	10.8	1.00	238.56	179.37	7.12	2017
620	0	1	4.5	1.00	239.56	179.37	7.12	2017
622	0	1	17.8	1.00	253.63	102.63	7.56	2017

623	0	2	10.8	1.00	261.92	14.60	7.64	2017
624	0	1	10.8	8.10	242.62	162.21	7.21	2017
625	0	2	6.4	8.10	242.62	162.21	7.21	2017
626	0	2	5.4	1.00	250.42	114.72	7.47	2017
627	0	2	10.8	7.59	250.98	116.12	7.45	2017
629	0	1	10.3	7.59	250.98	116.12	7.45	2017
631	0	2	22.5	7.59	250.98	116.12	7.45	2017
633	0	1	19.8	1.00	256.69	65.19	7.62	2017
634	0	2	7.2	1.00	256.81	70.17	7.57	2017
635	0	2	4.5	1.00	263.01	4.79	7.63	2017
636	0	1	13.4	1.00	262.06	16.20	7.63	2017
638	0	2	8.1	1.00	263.17	14.25	7.61	2017
639	0	2	14.4	1.00	263.17	14.25	7.61	2017
641	0	1	9	8.10	238.54	177.66	7.11	2017
642	0	1	5.4	1.00	239.54	177.66	7.11	2017
643	0	2	16	1.00	258.00	57.70	7.60	2017
644	0	2	4.5	1.00	258.00	57.70	7.60	2017
645	0	1	15.3	1.00	257.52	58.05	7.56	2017
646	0	1	10.8	1.00	257.52	58.05	7.56	2017
648	0	2	11.7	1.00	258.52	48.96	7.59	2017
649	0	3	18	1.00	258.52	48.96	7.59	2017
650	0	3	4.5	1.00	258.52	48.96	7.59	2017
651	0	2	21.6	1.00	262.82	1.00	7.63	2017
652	1	2	15.3	1.00	262.82	1.00	7.63	2017
653	0	2	4.5	1.00	263.51	25.62	7.63	2017
655	0	2	3.6	1.00	263.51	25.62	7.63	2017
657	0	3	11.7	1.00	262.51	36.12	7.44	2017
658	0	3	16.2	1.00	261.52	29.98	7.45	2017
659	0	3	19.8	1.00	262.52	29.98	7.45	2017
660	0	2	30.6	1.00	262.52	29.98	7.45	2017
661	0	3	9.9	1.00	261.66	37.33	7.49	2017
662	0	1	9	1.00	261.00	19.94	7.34	2017
664	0	2	16.2	1.00	261.00	19.94	7.34	2017
665	0	2	10.8	1.00	242.12	166.61	7.21	2017
666	0	2	5.4	1.00	242.12	166.61	7.21	2017
668	1	3	9.9	1.00	260.79	1.00	7.34	2017
670	0	1	14.4	1.00	261.47	9.48	7.66	2017
672	0	2	14.4	9.72	263.53	43.54	7.58	2017
673	0	1	23.4	9.72	263.53	43.54	7.58	2017
674	0	1	14	9.72	263.53	43.54	7.58	2017
675	0	2	6.3	9.72	263.53	43.54	7.58	2017
676	0	2	9.9	9.72	263.53	43.54	7.58	2017
677	0	3	12.6	13.03	263.20	51.89	7.54	2017
679	0	2	16.2	1.00	243.82	29.98	6.90	2017
681	0	2	12.6	1.00	238.84	36.92	6.81	2017
682	0	3	10.8	1.00	239.84	36.92	6.81	2017

684	0	2	19.8	1.00	239.84	36.92	6.81	2017
685	0	2	22.5	1.00	239.84	36.92	6.81	2017
686	0	1	8.1	1.00	239.84	36.92	6.81	2017
687	0	3	13.5	1.00	246.30	62.34	7.58	2017
689	0	3	15.3	1.00	247.30	62.34	7.58	2017
690	0	1	12.6	1.00	241.80	93.01	7.47	2017
691	0	2	6.3	1.00	241.80	93.01	7.47	2017
692	0	3	12.6	1.00	241.80	93.01	7.47	2017
693	0	1	9.9	1.00	240.86	94.15	7.54	2017
697	0	2	5.4	8.10	240.10	169.92	7.16	2017
699	0	3	16.2	1.00	241.10	169.92	7.16	2017
700	0	2	7.2	1.00	250.25	43.87	7.69	2017
701	0	2	13.5	1.00	250.25	43.87	7.69	2017
702	0	2	18	1.00	246.25	82.77	7.69	2017
703	0	1	25.2	1.00	246.25	82.77	7.69	2017
704	0	1	11.7	1.00	211.24	134.85	6.35	2017
705	0	2	19.8	1.00	211.24	134.85	6.35	2017
706	0	1	19.8	1.00	208.13	146.71	6.26	2017
709	0	3	16.2	0.13	247.96	87.69	6.83	2017
711	0	1	13.5	0.13	247.96	87.69	6.83	2017
712	0	2	14.4	1.00	255.10	92.77	7.24	2017
716	0	2	11	3.99	242.57	163.86	7.22	2017
717	0	2	8	3.99	242.57	163.86	7.22	2017
718	0	2	15.3	3.99	242.57	163.86	7.22	2017
719	0	1	18.9	3.99	242.57	163.86	7.22	2017
720	0	2	14.4	17.38	242.16	68.44	7.39	2017
721	0	1	16.3	1.00	255.68	1.00	7.66	2017
722	1	3	18	1.00	255.68	1.00	7.66	2017
725	1	2	18	1.00	255.56	28.76	7.73	2017
728	0	1	22.6	1.00	258.20	13.76	7.68	2017
730	0	1	14.4	1.00	257.20	13.76	7.68	2017
732	0	1	15.4	1.00	257.20	13.76	7.68	2017
734	0	2	20.7	1.00	260.22	45.69	7.68	2017
735	0	3	16.2	1.00	261.22	45.69	7.68	2017
736	0	2	9.9	1.00	262.04	68.59	7.62	2017
737	0	1	13.4	1.00	263.04	68.59	7.62	2017
738	0	2	9	1.00	262.36	61.09	7.66	2017
739	0	3	9	1.00	262.36	61.09	7.66	2017
740	0	1	19.8	1.00	262.36	61.09	7.66	2017
741	0	1	20.7	1.00	262.36	61.09	7.66	2017
742	0	1	19.5	1.00	262.36	61.09	7.66	2017
744	0	2	9	1.00	227.33	70.44	6.89	2017
745	0	1	12.5	1.00	244.04	156.35	7.27	2017
746	0	1	19.8	1.00	244.04	156.35	7.27	2017
749	0	3	3.6	19.65	224.81	66.28	6.82	2017
750	0	3	12.6	0.13	256.21	55.64	7.11	2017

752	0	1	9	0.13	256.21	55.64	7.11	2017
753	0	3	17.1	0.13	256.21	55.64	7.11	2017
757	0	3	16	1.00	263.13	62.97	7.64	2017
758	0	3	19.8	1.00	263.13	62.97	7.64	2017
759	0	2	9.9	1.00	263.13	62.97	7.64	2017
762	0	1	8.1	1.00	262.55	68.44	7.60	2017
763	0	1	15.3	1.00	246.10	115.30	6.80	2017
764	0	2	16.2	1.00	247.10	115.30	6.80	2017
765	0	1	3.6	1.00	247.73	132.83	7.36	2017
768	0	3	4.5	1.00	258.96	49.26	7.65	2017
771	0	1	17.5	1.00	247.49	40.66	6.92	2017
772	0	2	24.3	1.00	248.49	40.66	6.92	2017
775	0	2	12.6	1.00	252.05	17.82	7.06	2017
776	0	3	18.9	1.00	252.05	17.82	7.06	2017
777	0	1	30.6	1.00	252.05	17.82	7.06	2017
784	0	2	23.4	1.00	246.42	65.85	6.83	2017
786	0	2	18	1.00	246.42	65.85	6.83	2017
790	0	3	21.6	1.00	257.23	31.16	7.20	2017
791	0	1	8.1	1.00	253.63	1.00	7.35	2017
792	1	1	13.5	1.00	253.63	1.00	7.35	2017
793	1	2	21.5	1.00	252.63	1.00	7.35	2017
794	0	1	7.2	1.00	253.63	1.00	7.35	2017
795	0	2	28	1.00	256.33	81.63	7.67	2017
796	0	2	29	1.00	256.33	81.63	7.67	2017
797	0	1	14.7	1.00	256.33	81.63	7.67	2017
798	0	1	27	1.00	256.33	81.63	7.67	2017
800	0	1	27.9	1.00	256.33	81.63	7.67	2017
801	1	2	9.9	1.00	261.91	1.00	7.68	2017

SUPPLEMENTARY MATERIAL SECTION 3-CHAPTER VIII

Table S1. List of bird species found wasting food. We show if the species was observed wasting food in the experimental approach, in an area where the species is native or in an area where the species is exotic. We also show the region of origin of the species.

Species	Region	Experiment	Exotic	Native
Agapornis nigrigenis	Afrotropical	1	0	0
Agapornis personatus	Afrotropical	1	1	0
Agapornis roseicollis	Afrotropical	0	1	0
Agapornis taranta	Afrotropical	1	0	1
Alipiopsitta xanthops	Neotropical	0	0	1
Alisterus scapularis	Australasia	1	0	0
Amazona aestiva	Neotropical	0	1	1
Amazona albifrons	Neotropical	1	0	1
Amazona amazonica	Neotropical	0	1	1
Amazona auropalliata	Neotropical	0	0	1
Amazona autumnalis	Neotropical	0	0	1
Amazona barbadensis	Neotropical	1	0	0
Amazona finschi	Neotropical	1	0	0
Amazona guatemalae	Neotropical	0	0	1
Amazona lilacina	Neotropical	0	0	1
Amazona ochrocephala	Neotropical	0	1	1
Amazona oratrix	Neotropical	1	0	0
Amazona pretrei	Neotropical	0	0	1
Amazona tucumana	Neotropical	1	0	0
Amazona ventralis	Neotropical	0	0	1
Amazona vinacea	Neotropical	0	0	1

Amazona vitatta	Neotropical	0	0	1
Anodorhynchus hyacinthinus	Neotropical	0	0	1
Anodorhynchus leari	Neotropical	0	0	1
Ara ambiguus	Neotropical	0	0	1
Ara ararauna	Neotropical	0	1	1
Ara chloropterus	Neotropical	0	0	1
Ara macao	Neotropical	0	0	1
Ara militaris	Neotropical	0	0	1
Ara rubrogenys	Neotropical	1	0	1
Ara severus	Neotropical	0	0	1
Aratinga jandaya	Neotropical	1	0	1
Aratinga nenday	Neotropical	0	1	0
Aratinga solstitialis	Neotropical	1	0	0
Bolborhynchus lineola	Neotropical	1	0	0
Brotogeris chiriri	Neotropical	0	0	1
Brotogeris cyanoptera	Neotropical	1	0	0
Brotogeris jugularis	Neotropical	0	0	1
Brotogeris pyrrhoptera	Neotropical	0	0	1
Brotogeris versicolorus	Neotropical	0	1	1
Cacatua alba	Indomalaya	0	1	0
Cacatua galerita	Australasia	0	0	1
Cacatua moluccensis	Indomalaya	0	1	0
Calyptorhynchus banksii	Australasia	0	0	1
Calyptorhynchus funereus	Australasia	0	0	1
Cyanoliseus patagonus	Neotropical	1	0	1

Diopsittaca cumanensis	Neotropical	0	0	1
Diopsittaca nobilis	Neotropical	0	0	1
Eclectus roratus	Australasia	1	0	0
Enicognathus ferrugineus	Neotropical	0	0	1
Enicognathus leptorhynchus	Neotropical	0	0	1
Eupsittula aurea	Neotropical	0	0	1
Eupsittula cactorum	Neotropical	0	0	1
Eupsittula canicularis	Neotropical	0	1	1
Eupsittula nana	Neotropical	0	0	1
Eupsittula pertinax	Neotropical	0	0	1
Forpus coelestis	Neotropical	1	0	0
Lathamus discolor	Australasia	1	0	0
Melopsittacus undulatus	Australasia	0	1	0
Myiopsitta luchsi	Neotropical	0	0	1
Myiopsitta monachus	Neotropical	1	1	1
Neophema elegans	Australasia	1	0	0
Neophema pulchella	Australasia	1	0	0
Neophema splendida	Australasia	1	0	0
Neopsephotus bourkii	Australasia	1	0	0
Nymphicus hollandicus	Australasia	1	0	0
Ognorhynchus icterotis	Neotropical	0	0	1
Orthopsittaca manilata	Neotropical	0	0	1
Pionites melanocephalus	Neotropical	1	0	0
Pionus maximiliani	Neotropical	0	1	1
Pionus menstruus	Neotropical	0	0	1

Pionus senilis	Neotropical	1	0	1
Poicephalus meyeri	Afrotropical	0	0	1
Poicephalus robustus	Afrotropical	1	0	0
Poicephalus senegalus	Afrotropical	1	1	0
Polytelis swainsonii	Australasia	0	1	0
Primolius auricollis	Neotropical	0	0	1
Primolius couloni	Neotropical	0	0	1
Psephotus dissimilis	Australasia	1	0	0
Psephotus varius	Australasia	1	0	0
Psilopsiagon aymara	Neotropical	1	0	0
Psittacara chloropterus	Neotropical	0	0	1
Psittacara erythrogenys	Neotropical	0	1	1
Psittacara finschi	Neotropical	0	0	1
Psittacara frontata	Neotropical	0	0	1
Psittacara hockingi	Neotropical	0	0	1
Psittacara leucophtalmus	Neotropical	0	0	1
Psittacara mitratus	Neotropical	1	0	1
Psittacula alexandri	Indomalaya	1	0	0
Psittacula calthrapae	Indomalaya	0	0	1
Psittacula cyanocephala	Indomalaya	1	0	0
Psittacula eupatria	Indomalaya	0	0	1
Psittacula krameri	Indomalaya	1	1	1
Psittacara wagleri	Neotropical	0	0	1
Psittacus erithacus	Afrotropical	1	0	0
Pyrilia haematotis	Neotropical	0	0	1

Pyrrhura cruentata	Neotropical	1	0	0
Pyrrhura frontalis	Neotropical	0	0	1
Pyrrhura griseipectus	Neotropical	1	0	0
Pyrrhura molinae	Neotropical	1	0	1
Pyrrhura perlata	Neotropical	1	0	0
Thectocercus acuticaudatus	Neotropical	0	1	1
Trichoglossus haematodus	Australasia	0	0	1

Table S2. List of plant species where parrots wasted food. We show the species, family and the number of times we detected food wasting at the species.

Species	Family	Number of observations
Acacia angustissima	Fabaceae	16
Acacia aroma	Fabaceae	1
Acacia auriculiformis	Fabaceae	12
Acacia karroo	Fabaceae	13
Acacia mearnsii	Fabaceae	10
Acacia melanoxylon	Fabaceae	11
Acaena splendens	Rosaceae	1
Acrocomia totai	Arecaceae	65
Aesculus hippocastanum	Sapindaceae	1
Agonandra brasiliensis	Opiliaceae	2
Ailanthus altissima	Simaroubaceae	2
Aiphanes minima	Arecaceae	2
Aizoon canariense	Aizoaceae	1
Albizia carbonara	Fabaceae	1
Albizia guachapele	Fabaceae	2
Albizia julibrissin	Fabaceae	1
Albizia procera	Fabaceae	9
Albizia saman	Fabaceae	19
Anacardium excelsum	Anacardiaceae	3
Anacardium occidentale	Anacardiaceae	9
Anadenathera colubrina	Fabaceae	2
Anisocapparis speciosa	Capparidaceae	4
Annona muricata	Annonaceae	2

Arachis hypogaea	Fabaceae	36
Araucaria angustifolia	Araucariaceae	303
Araucaria araucana	Araucariaceae	34
Araucaria bidwillii	Araucariaceae	51
Araucaria cunninghamii	Araucariaceae	5
Arbutus unedo	Ericaceae	7
Ardisia escallonioides	Primulaceae	4
Asparagus arborescens	Asparagaceae	2
Aspidosperma quebracho-blanco	Apocynaceae	2
Astronium urundeuva	Anacardiaceae	1
Attalea butyracea	Arecaceae	2
Attalea phalerata	Arecaceae	0
Attalea princeps	Arecaceae	3
Attalea speciosa	Arecaceae	9
Attalea totai	Arecaceae	1
Averrhoa carambola	Oxalidaceae	3
Azadirachta indica	Meliaceae	2
Bactris gasipaes	Arecaceae	1
Bambusa vulgaris	Poaceae	4
Betula pendula	Betulaceae	4
Brachychiton populneus	Malvaceae	3
Brosimum alicastrum	Moraceae	1
Bucida buceras	Combretaceae	4
Bursera simaruba	Burseraceae	3
Bursera tomentosa	Burseraceae	2

Byrsonima crassifolia	Malpighiaceae	7
Byrsonima pachyphylla	Malpighiaceae	34
Byrsonima verbascifolia	Malpighiaceae	5
Cajanus cajan	Fabaceae	1
Callicarpa ampla	Lamiaceae	3
Calophyllum antillarum	Calophyllaceae	6
Carapa guianensis	Meliaceae	2
Carduus thoermeri	Asteraceae	112
Carya illinoinensis	Juglandaceae	7
Cassia javanica	Fabaceae	2
Castanea sativa	Fagaceae	3
Castilla elastica	Moraceae	1
Casuarina cristata	Casuarinaceae	1
Casuarina equisetifolia	Casuarinaceae	11
Catalpa bignonioides	Bignoniaceae	7
Cecropia peltata	Urticaceae	1
Cecropia schreberiana	Urticaceae	9
Cedrela odorata	Meliaceae	15
Cedrus atlantica	Pinaceae	1
Cedrus libani	Pinaceae	1
Ceiba pentandra	Malvaceae	28
Ceiba penthandra	Malvaceae	1
Ceiba speciosa	Malvaceae	9
Celtis australis	Ulmaceae	45
Centaurea solstitialis	Asteraceae	46

Cerastium glomeratum	Caryophyllaceae	3
Ceratonia siliqua	Fabaceae	5
Cercis siliquastrum	Fabaceae	67
Chenopodium murale	Chenopodiaceae	4
Cipadessa baccifera	Meliaceae	1
Citharexylum donnell-smithii	Verbenaceae	1
Citharexylum spinosum	Verbenaceae	7
Citrus × aurantium	Rutaceae	2
Citrus × sinensis	Rutaceae	37
Citrus aurantifolia	Rutaceae	1
Clusia pratensis	Clusiaceae	1
Cnidoscolus quercifolius	Euphorbiaceae	1
Coccoloba caracasana	Polygonaceae	1
Coccoloba uvifera	Polygonaceae	52
Cocos nucifera	Arecaceae	7
Coffea arabica	Rubiaceae	5
Commiphora leptophloeos	Burseraceae	1
Compsoneura sprucei	Myristicaceae	1
Condalia buxifolia	Rhamnaceae	8
Cordia alba	Boraginaceae	1
Cordia collococca	Boraginaceae	5
Cordia cymosa	Boraginaceae	1
Corymbia clarksoniana	Myrtaceae	7
Corymbia tessallaris	Myrtaceae	2
Couepia grandiflora	Chrysobalanaceae	15

Couepia polyandra	Chrysobalanaceae	1
Couma macrocarpa	Apocynaceae	2
Crataegus monogina	Rosaceae	1
Croton magdalenensis	Euphorbiaceae	1
Cupania americana	Sapindaceae	3
Cupressus sempervirens	Cupressaceae	87
Curatella americana	Dilleniaceae	16
Cyanophalla retusa	Capparidaceae	2
Cyperaceus sp.	Cyperaceae	1
Cyttaria harioti	Cyttariaceae	2
Delonix regia	Fabaceae	15
Dendropanax latilobus	Araliaceae	1
Dovyalis caffra	Salicaceae	47
Dracaena draco	Asparagaceae	2
Drimys winteri	Winteraceae	1
Elaeis guianensis	Arecaceae	1
Emmotum nitens	Icacinaeae	7
Eriobotrya japonica	Rosaceae	75
Erythrina caffra	Fabaceae	21
Erythrina fusca	Fabaceae	16
Erythrina poeppigiana	Fabaceae	10
Erythroxylum deciduum	Erythroxylaceae	6
Eucalyptus camaldulensis	Myrtaceae	45
Eucalyptus globulus	Myrtaceae	35
Eucalyptus miniata	Myrtaceae	5

Eucryphia cordifolia	Cunoniaceae	1
Eugenia uniflora	Myrtaceae	38
Ficus benghalensis	Moraceae	19
Ficus carica	Moraceae	115
Ficus insipida	Moraceae	2
Ficus lyrata	Moraceae	27
Ficus macrophylla	Moraceae	57
Ficus maxima	Moraceae	1
Ficus microcarpa	Moraceae	106
Ficus nymphaeifolia	Moraceae	1
Ficus religiosa	Moraceae	9
Ficus rubiginosa	Moraceae	16
Ficus sp.	Moraceae	1
Ficus stuhlmannii	Moraceae	6
Ficus trigonata	Moraceae	2
Flacourtia inermis	Salicaceae	5
Fraxinus angustigolia	Oleaceae	33
Geoffroea decorticans	Fabaceae	1
Gleditsia triacanthos	Fabaceae	18
Gliricidia sepium	Fabaceae	9
Gmelina arborea	Lamiaceae	15
Grevillea glauca	Proteaceae	3
Grevillea robusta	Proteaceae	91
Guarea guidonia	Meliaceae	27
Guazuma ulmifolia	Malvaceae	1

Hancornia speciosa	Apocynaceae	3
Handroantus chrysanthus	Bignoniaceae	2
Helianthus annuus	Asteraceae	99
Heliocarpus sp.	Malvaceae	1
Hibiscus rosa-sinensis	Malvaceae	4
Hirtella rugosa	Chrysobalanaceae	2
Hymenaea courbaril	Fabaceae	1
Hymenaea stigonocarpa	Fabaceae	17
Hypochaeris radicata	Asteraceae	2
Inga adenophylla	Fabaceae	1
Inga chocoensis	Fabaceae	1
Inga cylindrica	Fabaceae	3
Inga edulis	Fabaceae	1
Inga feuilleei	Fabaceae	1
Inga punctata	Fabaceae	1
Inga spectabilis	Fabaceae	11
Jacaranda mimosifolia	Bignoniaceae	39
Jatropha hieronymi	Euphorbiaceae	11
Jatropha humboldtiana	Euphorbiaceae	7
Jatropha mollisima	Euphorbiaceae	4
Juglans regia	Juglandaceae	3
Juniperus procera	Cupressaceae	1
Juniperus virginiana	Cupressaceae	9
Lagerstroemia indica	Lythraceae	2
Lagerstroemia speciosa	Lythraceae	9

Laureliopsis philippiana	Atherospermataceae	2
Leucaena leucocephala	Fabaceae	2
Ligustrum japonicum	Oleaceae	38
Ligustrum lucidum	Oleaceae	13
Livistona chinensis	Arecaceae	165
Luehea seemannii	Malvaceae	4
Magonia pubescens	Sapindaceae	2
Malus domestica	Rosaceae	17
Mangifer indica	Anacardiaceae	96
Mangifera zeylanica	Anacardiaceae	1
Manilkara bidentata	Sapotaceae	3
Maprounea guianensis	Euphorbiaceae	2
Maranthes panamensis	Chrysobalanaceae	7
Mauritia flexuosa	Arecaceae	46
Mauritiella armata	Arecaceae	1
Maytenus boaria	Celastraceae	5
Melaleuca citrina	Myrtaceae	17
Melia azedarach	Meliaceae	311
Melicoccus bijugatus	Sapindaceae	10
Miconia impetiolaris	Melastomataceae	10
Misodendrum linearifolium	Misodendraceae	2
Morus alba	Moraceae	84
Morus nigra	Moraceae	127
Mouriri pusa	Melastomataceae	2
Musa × paradisiaca	Poaceae	3

Myrceugenia exsucca	Myrtaceae	1
Myrtus communis	Myrtaceae	16
Neea theifera	Nyctaginaceae	16
Nephelium lappaceum	Sapindaceae	1
Nothofagus dombeyi	Nothofagaceae	3
Nothofagus obliqua	Nothofagaceae	10
Ochroma pyramidale	Malvaceae	1
Olea europaea	Oleaceae	49
Olea europaea sylvestris	Oleaceae	21
Onopordum acanthium	Asteraceae	1
Oryza sativa	Poaceae	11
Pachira quinata	Malvaceae	10
Parkia biglandulosa	Fabaceae	4
Parkinsonia aculeata	Fabaceae	3
Parkinsonia praecox	Fabaceae	1
Parodiodendron marginivillosum	Picrodendraceae	2
Passiflora edulis	Passifloraceae	2
Patellifolia patellaris	Amaranthaceae	5
Patellifolia procumbens	Amaranthaceae	1
Peltophorum pterocarpum	Fabaceae	1
Persea americana	Lauraceae	11
Phalaris canariensis	Poaceae	3
Phoenix canariensis	Arecaceae	260
Phoenix dactylifera	Arecaceae	437
Phytolacca dioica	Phytolaccaceae	33

Pinus pinea	Pinaceae	13
Pinus radiata	Pinaceae	7
Pithecellobium dulce	Fabaceae	9
Plantago lanceolata	Plantaginaceae	2
Platanus × hispanica	Platanaceae	68
Platanus orientalis	Platanaceae	1
Platimiscium curuense	Fabaceae	1
Platypodium elegans	Fabaceae	1
Plocama pendula	Rubiaceae	5
Populus alba	Salicaceae	45
Populus deltoides	Salicaceae	33
Populus nigra	Salicaceae	31
Populus tremuloides	Salicaceae	3
Pouteria ramiflora	Sapotaceae	31
Prestoea montana	Arecaceae	6
Prosopis alba	Fabaceae	15
Prosopis caldeana	Fabaceae	2
Prosopis kuntzei	Fabaceae	4
Prunus avium	Rosaceae	47
Prunus cerasifera	Rosaceae	35
Prunus cerasus	Rosaceae	18
Prunus domestica	Rosaceae	6
Prunus dulcis	Rosaceae	135
Prunus malus	Rosaceae	1
Prunus persica	Rosaceae	17

Prunus salicina	Rosaceae	6
Pseudobombax septenatum	Malvaceae	6
Pseudosamanea guachapele	Fabaceae	1
Psidium cattleianum	Myrtaceae	1
Psidium guajava	Myrtaceae	26
Pterodon emarginatus	Fabaceae	1
Punica granatum	Lythraceae	16
Pyrus bourgaeana	Rosaceae	11
Pyrus communis	Rosaceae	25
Qualea amoena	Vochysiaceae	3
Quercus ilex	Fagaceae	3
Rhaphithamnus spinosus	Verbenaceae	1
Rheedia achachairu	Clusiaceae	2
Ribes magellanicus	Grossulariaceae	1
Richeria grandis	Phyllanthaceae	24
Robinia pseudoacacia	Fabaceae	35
Roystonea borinquena	Arecaceae	60
Sabal domingensis	Arecaceae	1
Salix alba	Salicaceae	1
Salix babylonica	Salicaceae	3
Salix caprea	Salicaceae	2
Salvertia convallariodora	Vochysiaceae	1
Samanea saman	Fabaceae	1
Sapium saltense	Euphorbiaceae	2
Saribus rotundifolius	Arecaceae	7

Schefflera actinophylla	Araliaceae	1
Schinopsis lorentzii	Anacardiaceae	21
Schinopsis marginata	Anacardiaceae	1
Schinus molle	Anacardiaceae	77
Schinus sp.	Anacardiaceae	1
Schinus terebinthifolius	Anacardiaceae	37
Sclerolobium aureum	Fabaceae	3
Senegalia gilliesii	Fabaceae	1
Senna siamea	Fabaceae	8
Serjania polyphylla	Sapindaceae	3
Silybum marianum	Asteraceae	52
Simarouba amara	Simaroubaceae	27
Sonchus tenerrimus	Asteraceae	3
Spathodea campanulata	Bignoniaceae	148
Spondias dulcis	Anacardiaceae	9
Spondias mombin	Anacardiaceae	1
Spondias purpurea	Anacardiaceae	8
Sterculia apetala	Malvaceae	7
Sterculia balanghas	Malvaceae	4
Sterculia foetida	Malvaceae	4
Styphnolobium japonicum	Fabaceae	58
Swartzia jorori	Fabaceae	1
Syagrus coronatus	Arecaceae	5
Syagrus romanzoffiana	Arecaceae	7
Syzygium malaccense	Myrtaceae	5

Syzygium smithii	Myrtaceae	8
Tabebuia rosea	Bignoniaceae	4
Tamarindus indica	Fabaceae	138
Tamarix gallica	Tamaricaceae	5
Tapirira guianensis	Anacardiaceae	3
Tapirira obtusa	Anacardiaceae	1
Taraxacum officinale	Asteraceae	3
Tebebuia impetiginosa	Bignoniaceae	1
Tectona grandis	Verbenaceae	5
Terminalia bucidoides	Combretaceae	2
Terminalia catappa	Combretaceae	87
Terminalia muelleri	Combretaceae	3
Terminalia sericea	Combretaceae	6
Terminalia sericea	Combretaceae	1
Thespesia grandiflora	Malvaceae	8
Thespesia populnea	Malvaceae	1
Thevetia peruviana	Apocynaceae	1
Tipuana tipu	Fabaceae	17
Toona ciliata	Meliaceae	5
Trachycarpus fortunei	Arecaceae	3
Trifolium repens	Fabaceae	1
Ulmus minor	Ulmaceae	29
Vallesia glabra	Apocynaceae	1
Vassobia breviflora	Solanaceae	1
Vitex cymosa	Lamiaceae	0

Vitex gigantea	Lamiaceae	1
Vochysia divergens	Vochysiaceae	1
Vochysia ferruginea	Vochysiaceae	3
Vochysia pilosa	Vochysiaceae	1
Vochysia tucanorum	Vochysiaceae	2
Washingtonia filifera	Arecaceae	147
Washingtonia robusta	Arecaceae	87
Ximenia americana	Olacaceae	1
Zea mays	Poaceae	12
Ziziphus joazeiro	Rhamnaceae	2
Ziziphus mauritiana	Rhamnaceae	1
Ziziphus mistol	Rhamnaceae	6
Zygia latifolia	Fabaceae	0

Table S3. Results of the model relating the proportion of food wasted in the experiment in relation to the average body mass of the parrot species, the number of individuals in the cage during the experiment and the presence of a fasting period before the trial. We show the model coefficient of the variable and the p-value.

Variable	**Coefficient**	**P-value**
Weight	-0.1195	0.14
Fasting presence	-0.0989	0.16
Number of individuals	-0.0397	0.78

Table S4. Summary of the number of fruits/seeds found under a tree after a group of parrots foraged on it. We include information on the total number of trees counted, mean (± SD) and maximum number of fruits/seeds found behind the trees, and mean (± SD) and maximum number of intact and half-eaten fruits/seeds.

	Fruits	**Seeds**
Number trees counted	57	72
Number fruits/seeds per tree	53.4 ± 53.2	41.98 ± 54.9
Intact	23.28 ± 29.44	13.8 ± 27.53
Maximum	164	130
Half-eaten	27.5 ± 25.7	11.4 ± 33.6
Maximum	92	239

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