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Nesting innovations allow population growth in an invasive population of rose-ringed parakeets

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Abstract

Certain traits of recipient environments, such as the availability of limiting resources, strongly determine the establishment success and spread of non-native species. These limitations may be overcome through behavioral plasticity, allowing them to exploit alternative resources. Here, we show how a secondary cavity nester bird, the rose-ringed parakeet *Psittacula krameri*, innovates its nesting behavior as a response to the shortage of tree cavities for nesting in its invasive range in Tenerife (Canary Islands). We observed that some breeding pairs excavated their own nest cavities in palms, thus becoming primary cavity nester, whereas others occupied nests built with wood sticks by another invasive species, the monk parakeet *Myiopsitta monachus*. The use of these novel nesting strategies increased the number of breeding pairs by up to 52% over 6 years, contributing to a 128.8% increase of the whole population. Innovative nests were located at greater heights above ground and were more aggregated around conspecifics but did not result in greater breeding success than natural cavities. Occupation of monk parakeet colonies by rose-ringed parakeets also benefited the former species through a protective-nesting association against nest predators. Our results show how an invasive species innovate nesting behaviors and increase nest-site availability in the recipient environment, thus facilitating its population growth and invasion process. Potential behavioral innovations in other invasive rose-ringed parakeet populations may be overlooked, and should be considered for effective management plans.

Key words: antipredator response, behavioral flexibility, biological invasions, cavity nesters, nesting innovation, reproductive success.

Behavioral flexibility is a form of phenotypic plasticity in which individuals change their behavior to adaptively cope with environmental changes (Piersma and Drent 2003; Dingemanse et al. 2010). Flexibility may arise through innovation when an individual develops a new behavior, or through social learning and copying, by adopting the behaviors of others (Fragaszy and Perry 2003). When innovating, individuals can increase the availability of a particular type of resource (Reader and Laland 2003), such that innovations can arise not only as a consequence of opportunity but also by necessity (Morand-Ferron et al. 2011; Lee and Moura 2015). Many examples of innovative behavior focus on the acquisition and transmission of novelty in the context of food rewards (Overington et al. 2011; Ducatez et al. 2015; Johnson-Ulrich et al. 2019; Wang and Liu 2021). However, despite its higher degree of specialization (Hansell 1984), there are also examples of changes in nesting habits in some species, mainly the use of unusual material or sites (Blanco

et al. 1997; Nicolakakis and Lefebvre 2000; Tagg et al. 2013; Tella et al 2014; Yosef et al. 2019).

Most innovative behaviors of birds focus on food and nesting sites and materials (Lefebvre et al. 2004), as the main resources limiting populations (Newton 1998). For secondary cavity nesters, which depend on pre-existing cavities that either form naturally or are previously dug by primary cavity excavators (Newton 1994; Martin and Eadie 1999), cavities are often a limiting resource, and their availability and suitability can drive their population dynamics (Gibbons and Lindenmayer 2002; Aitken and Martin 2008; Banda and Blanco 2009; Lindenmayer et al. 2014; Stojanovic et al. 2016). When introduced into new areas, non-native secondary cavity nesters can only establish where there are available cavities (Pell and Tidemann 1997; Strubbe and Matthysen 2007) or if they can outcompete native species by efficiently exploiting this and other resources through aggressive behaviors (Pell and Tidemann 1997; Koenig 2003; Wiebe 2003, Harper et al. 2005, Strubbe and Matthysen 2009; Orchan et al. 2013; Hernández-Brito et al. 2014a, 2018). Some non-native species may also develop innovative behaviors to increase resource availability in the recipient environment and successfully establish (Sol and Lefebvre 2000; Sol et al. 2002; Wright et al. 2010). Indeed, the frequency of innovative behaviors has been positively correlated with the relative brain size of species and identified as a good predictor of establishment success of past deliberate avian introductions (Sol et al. 2005; but see: Abellán et al. 2017).

Large-brained species like parrots (Aves Psittaciformes) show wide behavioral plasticity in foraging strategies and food exploited seasonally over large areas owing to high mobility (Renton et al. 2015; Blanco et al. 2018). This versatility may have allowed them to become successful invaders after human introduction worldwide (Calzada Preston and Pruett-Jones 2021). Because most parrots are secondary cavity nesters, the availability of pre-existing cavities is a major limiting factor that determines habitat suitability (Renton et al. 2015). The availability of cavities is even more important as it can affect breeding densities, especially for species nesting socially and forming nest clusters to large colonies. The rose-ringed parakeet *Psittacula krameri* is one of the most widespread invasive bird species in the world (Calzada Preston and Pruett-Jones 2021) and is considered among the 100 worst alien species in Europe (DAISIE 2009; Jackson 2021). As a secondary cavity nester, rose-ringed parakeets depend on pre-existing tree cavities to breed, out-competing native species in invaded areas (Strubbe and Matthysen 2009; Strubbe et al. 2010; Peck et al. 2014; Hernández-Brito et al. 2014a, 2018; Yosef et al. 2016; Jackson 2021; Mori and Menchetti 2021). Some individuals in invasive and native populations use alternative nesting structures such as building walls (Lamba 1966; Hernández-Brito et al. 2014a; Grandi et al. 2018) or modify pre-existent tree cavities (Hernández-Brito et al. 2014a; Menchetti et al. 2016), which can be indicative of nesting habitat saturation and a shortage of suitable cavities.

Here, we show the emergence and consolidation of 2 novel nesting behaviors in an invasive rose-ringed parakeet population in Tenerife (Canary Islands, Spain). These innovations include the excavation of nests (tree cavities) and the use of chambers within the colonial nests of the monk parakeet *Myiopsitta monachus* (Figure 1), the only parrot species that builds its own nests (Hernández-Brito et al. 2021a). These nests are made of branches and are also used permanently as roosting sites. To our knowledge, these nesting behaviors have not been previously described in the native nor the invaded range of the species (Lamba 1966,

Jackson 2021), thus we consider them as innovative. We hypothesized that these nesting innovations have appeared and increased in number due to the reduction in the availability of natural tree cavities, allowing population growth. To test this hypothesis, we monitored the breeding population of the species during 6 consecutive breeding seasons, taking into account the annual availability of cavities in the area and their characteristics. We discuss the largely overlooked ability of invasive species to develop innovative behaviors to overcome restrictions in the recipient environments, and its implications in the invasion process.

Materials and methods

Study area and species

Most of the natural vegetation of Tenerife (e.g., coastal shrub and thermophilus and laurel forests) has been dramatically altered over the years and, today, most of the island is dominated by rural or urban areas (del Arco Aguilar et al. 2010). In these transformed areas, several non-native avian species of the Orders Galliformes, Columbiformes, Psittaciformes, and Passeriformes have been reported as introduced, with 5 of them (Barbary partridge *Alectoris barbara*, Barbary dove *Streptopelia roseogrisea*, Monk parakeet, Rose-ringed parakeet, and Nanday parakeet *Nandayus nenday*) showing self-sustaining populations (Garcia-del-Rey 2018). Additionally, an incipient but growing non-congeneric population of hybrids between the non-native orange-winged Amazon *Amazona amazonica* and scaly-headed parrot *Pionus maximiliani* is present on the island (Hernández-Brito et al. 2021b; Figure 2).

Rose-ringed parakeets were first recorded in Tenerife in the mid-1980s (Martín and Lorenzo 2001), with a large, but unknown, number of individuals deliberately released in 2002 (D. Hernández-Brito, unpublished data). By 2019, we recorded 3 isolated populations summing ca. 550 individuals established in different urban areas of the island (Figure 2), with one of them subjected to a control program since 2017 (Figure 2, Area IV). Our study was focused on the largest rose-ringed parakeet population of the island, located in the municipality of Arona (altitude: 20 m a.s.l.; Figure 2, Area I), with ca. 350 individuals in 2019. Moreover, the largest monk parakeet population of the island is established in the same area (ca. 160 individuals in 2019; Figure 2). This urbanized area is surrounded by volcanic fields covered by coastal shrubs, so ornamental trees such as fig trees (*Ficus* spp) and palm trees (*Phoenix* spp and *Washingtonia* spp) present in the urban area are the only available nesting sites for parakeets. However, these trees are barely mature (Palomino and Carrascal 2005), and there are no primary cavity nesters in these areas (Martín and Lorenzo 2001; Garcia-del-Rey 2018); thus cavities are only formed by tree decay and are expected to be naturally scarce.

Field procedures

During the breeding seasons (from late December to late May) of the period 2014–2019, we censused and located with global positioning system (GPS; ±3 m) all rose-ringed and monk parakeet nests, as well as all tree cavities available in the area. We performed repeated visits to each site to assess its occupation (confirmed when we observed adults in the nests, at least on 10 different days), and record breeding success (i.e., breeding pairs successfully producing at least one fledgling) following Hernández-Brito et al. (2014a). Rose-ringed parakeet nests were classified into 2 categories according to their origin: natural (pre-existing tree cavities), and innovative
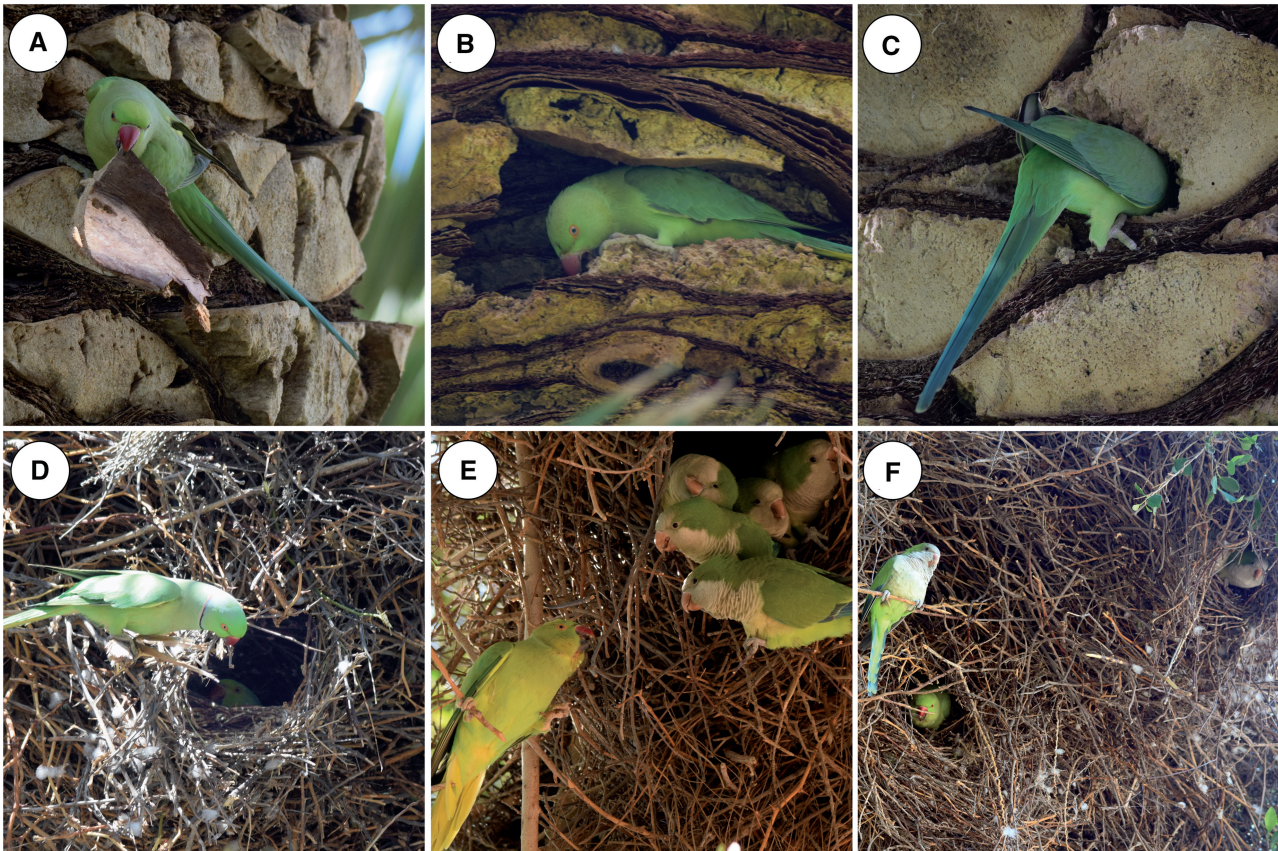
Figure 1 Innovative nesting behaviors recorded in an invasive rose-ringed parakeet population established in Tenerife (Canary Islands, Spain). (A–C) Rose-ringed parakeets excavating nesting cavities in the trunks of Canary Island date palms *Phoenix canariensis*. (E and F) rose-ringed parakeets nesting in monk parakeet nests. Pictures: Dailos Hernández-Brito.

(excavated cavities or chambers within monk parakeet nests). We visually estimated the height above ground (in meters) and the width of each cavity entrance (in centimeters), which was scored as small (S; <4 cm), medium (M; 4–8 cm) or large, (L; >8 cm) following Hernández-Brito et al. (2014a). Using the GPS locations of all cavities and monk parakeet nests, we calculated an annual aggregation index relative to the spatial distribution of all rose-ringed parakeet breeding pairs and among breeding pairs using innovative nests (excavated cavities and chambers within monk parakeet nests). This index, which reflects conspecific density, was obtained as $\Sigma \exp(-d_{ij})$ (with $i \neq j$), where d_{ij} was the linear distance between cavities i and j (Hernández-Brito et al. 2020).

During censuses, we also devoted 780 h to recording individual behaviors, mainly those related to the excavation of cavities (360 h), but also interspecific aggressions between rose-ringed and monk parakeets and toward nest predators during the occupation of and establishment in monk parakeet colonies by rose-ringed parakeet (445 h). Moreover, we assessed these anti-predator responses displayed by rose-ringed and monk parakeets in their nests both cooperatively and separately.

Statistical analysis

We used generalized linear models to relate the annual number of new innovative nests (response variable; Poisson error distribution; and log link function) to the number of available (non-used) cavities (explanatory variable). To ascertain differences in nest site characteristic, we compared their entrance size, height, and conspecific density (response variables) among used and non-used natural cavities and innovative nesting sites (excavated cavities and chambers within monk parakeet nests; fixed factor). Thus, we employed an ordinal logistic regression for entrance size, a linear model for height above the ground, and a linear mixed model for aggregation within the breeding population (including year and nest as random terms), applying a Tukey post hoc test (package *lsmeans*; Lenth 2016). Moreover, we assessed which characteristics of monk parakeet nests (height above the ground, total number of chambers, and aggregation index within the rose-ringed parakeet breeding population; included as explanatory variables) affect their occupancy by rose-ringed parakeets by modeling the annual occupation of monk parakeet colonies by rose-ringed parakeets through generalized linear mixed models (response variable; binomial error distribution, logit link function; including colony as a random term).

To understand the fitness consequences of this innovative behavior, we first assessed the role played by nest characteristics (entrance size, height, and conspecific density; included as explanatory variables) in improving breeding success using generalized linear mixed models (response variable, binomial error distribution, logit link function, year and nest included as random terms). Using the same model structure, we then compared the breeding success of rose-ringed parakeets using innovative nests with that of breeding pairs in natural cavities (explanatory variable).

The model selection was performed using the Akaike information criterion corrected (AICc) for small sample sizes (Burnham and Anderson 2002). Within each set of models (which includes the null
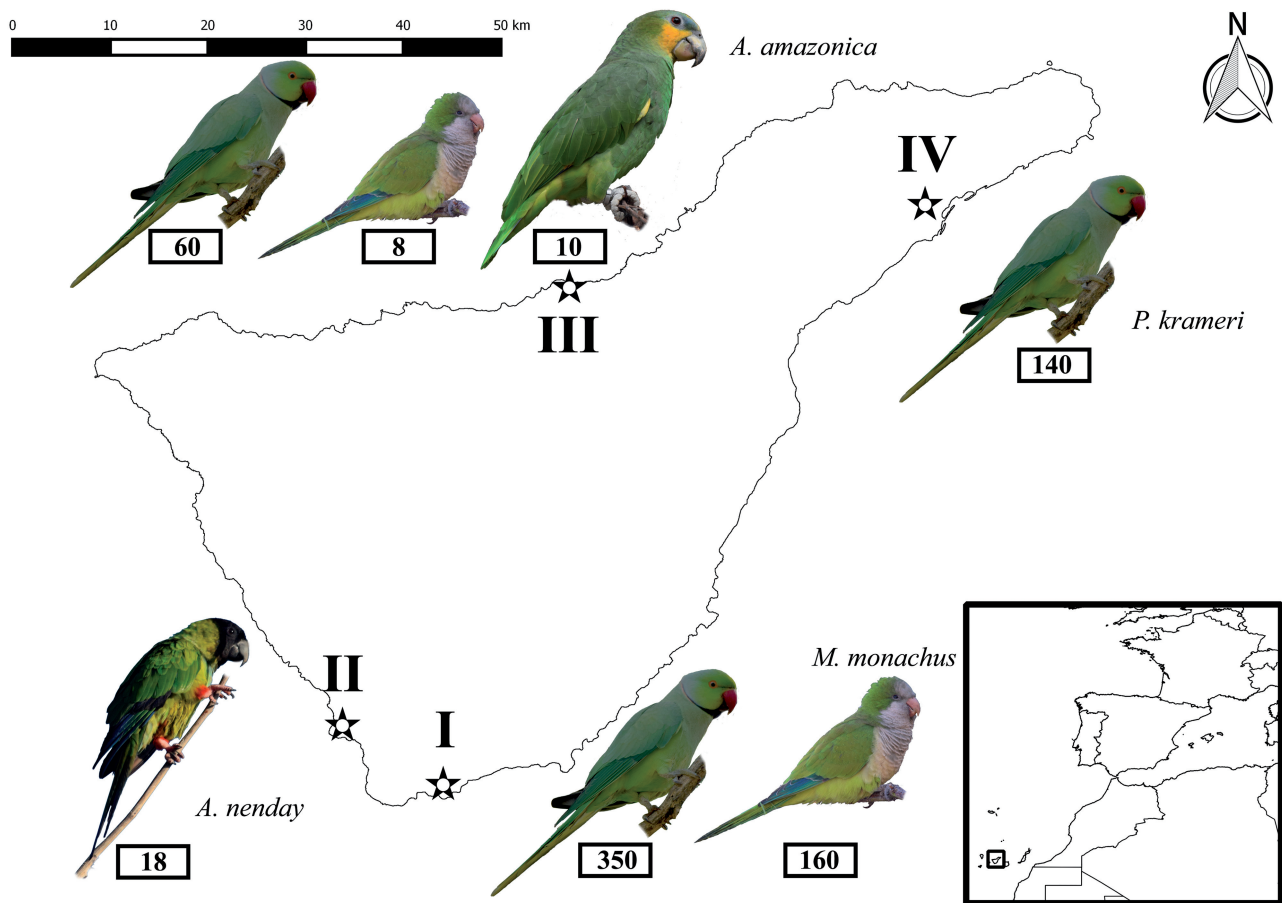
Figure 2 Estimated number of non-native parrot populations established in 4 areas (I–IV) of Tenerife (Canary Islands) after the 2019 breeding season: rose-ringed parakeet *Psittacula krameri*, monk parakeet *Myiopsitta monachus*, nanday parakeet *Aratinga nenday*, and orange-winged parrot *Amazona amazonica*. Pictures: Dailos Hernández-Brito.

model), we calculated the ΔAICc (as the difference between the AICc of model *i* and that of the best model) and the Akaike weight (*w*) of each model. Models within 2 AICc units of the best one were considered as innovative (package glmmTMB; Magnusson et al. 2017).

Finally, we assessed potential differences in the efficiency of anti-predator behavior shown by both parakeet species through a chi-square 2-sample test to compare the frequencies of successful nest defense events by rose-ringed parakeets and monk parakeets alone, and by cooperation between the 2 parakeet species. All statistical analyses were conducted in R version 4.0.3 (R Development Core Team 2020).

Results

Characteristics of innovative nests and nesting behavior

During the study period, we recorded 65 events of rose-ringed parakeets excavating cavities (Figures 1A–C and 3B) in the soft parts of the trunk and canopy base of 3 different palm species, namely, the Canary Island date palm *Phoenix canariensis*, the date palm *Phoenix dactylifera* and the California fan palm *Washingtonia filifera*. Female rose-ringed parakeets mainly performed those excavations in the middle of the laying period (late January and February), starting from scratch (i.e., not using previous holes in the surface of the palm trees) and investing from 10 to 90 min/day and 2–5 days to

complete them. Most of these cavities (61.1%) were located in the canopy base (Figure 1A, B), where parakeets remove the dry leaf petioles to excavate a short tunnel, although they can also directly dig into the trunks of palm trees, below the canopy base (36.9%; Figure 1C). In only 7 cases (ca. 11%) did individuals abandon excavation without finishing the nest cavity.

We recorded 37 events of rose-ringed parakeets breeding in chambers of 24 different monk parakeet nests, mostly active ones (62.5%; Figures 1D–F and 3B). Monk parakeet colonies were mainly located on Indian laurels *Ficus microcarpa* and the same palm tree species observed in excavated nests, 48 and 44% of the total, respectively. These nests were occupied between late December and February, despite the active defense of monk parakeets.

Antipredatory behavior

During the first 4–7 days after a rose-ringed parakeet pair began to use a monk parakeet chamber (Figure 1D), we recorded a total of 54 aggressions between the 2 parakeet species (Figure 1E), lasting between 5 and 37 min. Rose-ringed parakeets won most of these fights (61% of the total aggressions), all started by monk parakeets defending their nests. Rose-ringed parakeets ultimately usurped and occupied all these nest chambers. After that, no more aggressive interactions were detected (Figure 1F) but, strikingly, both species cooperated during nest defense against nest predators (i.e., black rats *Rattus rattus*, European kestrels *Falco tinnunculus*, and

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Mediterranean yellow-legged gulls *Larus michahellis*). This cooperative nest defense allowed the expulsion of the predator in 88% of 25 recorded cases, a value significantly higher ($\chi^2 = 8.69$, $P = 0.003$) than that observed when monk parakeets defended their colonies alone (46.9% of the 32 observations of monk parakeets attacking rats or kestrels resulted in the expulsion of the predator). Although we did not record rose-ringed parakeets defending monk parakeet colonies alone, we recorded nest defense against the same predator species in nests located in tree cavities, of which, 85.7% of 35 events resulted in their expulsion. Thus, differences between whether or not there was cooperative defense were not significant for rose-ringed parakeets ($\chi^2 = 7.01e$-31, $P = 1$), being just as successful in cooperation with monk parakeets as alone.

Population trends and use of innovative nests

From 2014 to 2019, rose-ringed parakeets increased from 31 to 85 breeding pairs in the study area, with a growing percentage of breeding pairs occupying innovative nests (from 13% in 2014 to 52% in 2019; Figure 3A) as the number of available cavities declined (estimate: -0.09, Standard error (SE): 0.01, $t = -6.42$, $P < 0.0001$; Figure 3C). Consequently, the rose-ringed parakeet population grew by 128.8% from 153 individuals (2014) to 350 individuals (2019), growing at a rate of 21.5% per year. Innovative nests (87 out of the 135 nesting sites) were occupied for an average of 2.53 years (range: 1–6 years), although we could not assess the identity of breeding individuals. Excavated nests were not abandoned in successive breeding seasons; only their destruction after tree-felling (i.e., by human activity or storms) or physical deterioration prevented their reuse. However, 25% of rose-ringed parakeet nests located in monk parakeet colonies ended their occupation in subsequent breeding seasons even though these chambers were still available.

Innovative nesting sites were the tallest and the most aggregated within the breeding population (Table 1 and Figure 4). Natural cavities used by parakeets were intermediate in height and aggregation, while non-used cavities were located at the lowest height, more isolated in terms of the location of breeding pairs, and had slightly larger entrances (Table 1 and Figure 4). Monk parakeet colonies used by rose-ringed parakeets were the largest (in terms of number of chambers; estimate: 0.45, SE: 0.18, $z = 6.05$, $df = 1$, $P = 0.0139$) and the closest (i.e., more aggregated: estimate: 0.07, SE: 0.03, $z = 4.24$, $P = 0.0396$) to other active rose-ringed parakeet nests. Height was not a significant predictor of colony use by rose-ringed parakeets (estimate: 0.23, SE: 0.16, $z = 2.16$, $P = 0.1418$; Supplementary Tables S1 and S2).

Breeding success

Breeding success was not related to any of the variables considered (i.e., the height above the ground, the entrance size, or the aggregation within the breeding population; Supplementary Table S3), nor when considering whether they bred in innovative nesting-sites or natural cavities (Supplementary Tables S4 and S5).

Discussion

Behavioral innovations can be beneficial for species to adjust to environmental changes (Wang and Liu 2021), as well as to assist the establishment and spread of invasive species in their recipient environments (Sol et al. 2002; Martin and Fitzgerald 2005). Innovativeness is generally assumed to increase fitness through enhanced survival or reproductive
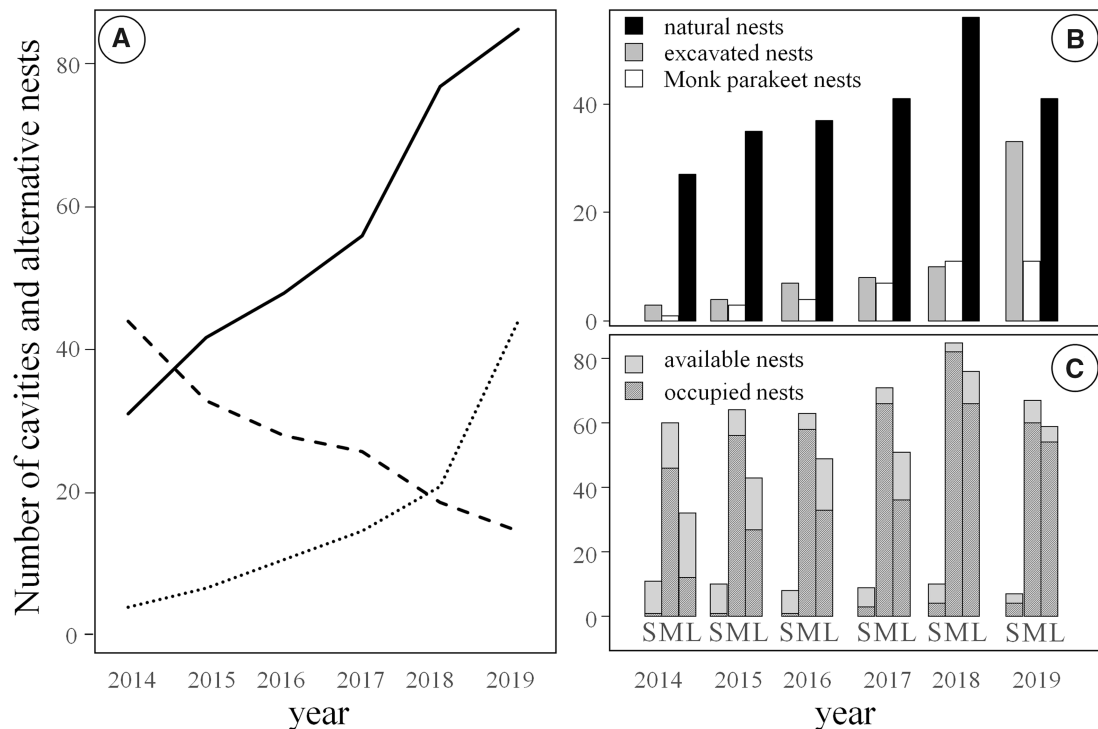
Figure 3 (A) Number of nests of rose-ringed parakeets (solid line), innovative nesting sites used by the species (dotted line), and nonused, available cavities (dashed line) recorded during the study period. (B) Number of natural and innovative nests (excavated nests and chambers within monk parakeet nests) used from 2014 to 2019. (C) Number of cavities available and used by rose-ringed parakeets during the study period in terms of their entrance sizes (small, medium, and large).

Table 1 Differences in entrance size, height above the ground, and aggregation within the breeding population among the different nesting sites used and available (fixed factor "nest sites", 3 levels: innovative nesting sites, and natural cavities used and non-used) for rose-ringed parakeets in Tenerife (Canary Islands) from 2014 to 2019

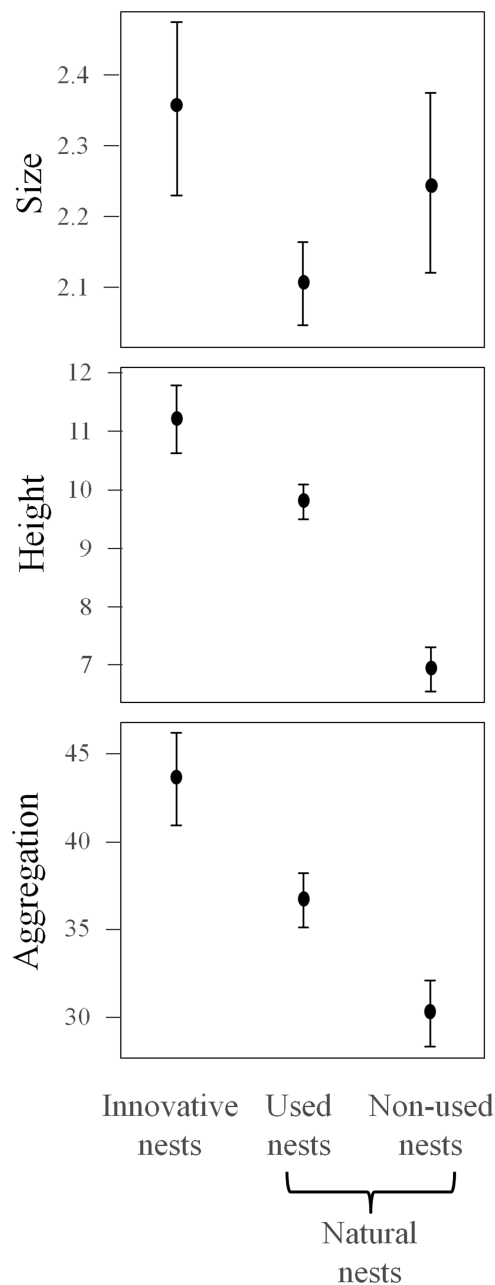| Contrasts	Estimate	SE	t	P-value
Size~Nest site: $\chi^2 = 5.19$, $df = 2$, $P = 0.0748$				
Innovative nesting sites—used natural cavities	0.18	0.2	0.9	1.0000
Innovative nesting sites—nonused natural cavities	−0.31	0.22	−1.37	0.5136
Used natural cavities—nonused natural cavities	−0.49	0.22	−2.27	0.0695
Height~Nest site: $\chi^2 = 212.47$, $df = 2$, $P < 0.0001$				
Innovative nesting sites—used natural cavities	1.27	0.27	4.64	<0.0001
Innovative nesting sites—nonused natural cavities	3.96	0.28	14.23	<0.0001
Used natural cavities—nonused natural cavities	2.69	0.27	9.92	<0.0001
Aggregation within the breeding population~Nest site: $\chi^2 = 99.74$, $df = 2$, $P < 0.0001$				
Innovative nesting sites—used natural cavities	7.53	1.36	5.548	<0.0001
Innovative nesting sites—nonused natural cavities	13.79	1.38	9.976	<0.0001
Used natural cavities—nonused natural cavities	6.26	1.35	4.642	<0.0001

The significance of the contrasts was corrected using Bonferroni's correction.

success (Sol 2009; Sol et al. 2016). However, direct evidence supporting these assumptions is scarce (Keagy et al. 2009; Cauchard et al. 2013; Preiszner et al. 2017; Wetzel 2017; Yosef et al. 2019) and not always conclusive (Cole et al. 2012; Cole and Quinn 2012; Isden et al. 2013). According to our results, the breeding success of individuals was not affected by the characteristics or the type of nesting site used (innovative nesting sites or natural cavities), suggesting that the main benefit of these innovative behaviors does not arise through a higher success of pairs using them but through increasing the possibility of breeding in the absence of adequate natural cavities. Although different factors can be simultaneously operating, the lack of differences in the breeding success observed among pairs using innovative nests and natural cavities suggests that this behavior is not mostly performed by young individuals that are generally poorer breeders (Clutton-Brock 1988), often delaying reproduction when the population is saturated (van de Pol and Verhulst 2006; Brown 2014). More likely, innovating individuals may have particular behavioral traits (e.g.,less neophobic, bolder, or more risk-tolerant; Webster and Lefebvre 2001; Overington et al. 2011; Benson-Amram and Holekamp 2012; Audet et al. 2016; van Horik et al. 2017; Johnson-Ulrich et al. 2018), which may allow them to innovate in their nesting habits when optimal nesting resources are scarce (Quinn et al. 2003; Hernández-Brito et al. 2020).

Innovative behaviors occur primarily when innovators are able to invent novel strategies or copy them by observing conspecifics (Reader and Laland 2003). Because there were no marked individuals in our study, we cannot determine which of these mechanisms is driving all innovator rose-ringed parakeets in the spread of novel nesting strategies in the population. Indeed, the innovative nesting sites were located in areas with the highest densities of conspecific nests, so social transmission of novel behaviors among conspecific would be more likely. Besides, the wide range of movements of rose-ringed parakeets, ca. 6–9 km/day or even up to 24 km (Pârâu et al. 2016), together with the fact that they concentrate on communal roosts, which are considered to be centers of social learning and information sharing (Salinas-Melgoza et al. 2013; Hobson et al. 2014; Toft and Wright 2015), may facilitate the diffusion of novel behaviors within the population (Claidière et al. 2013; Kulahci et al. 2016; Lambert et al. 2019). Cultural transmission can be also picked up by nonbreeding parakeets regularly prospecting the vicinity of active nests (Renton et al. 2015), mainly at the small spatial scale of our study population. However, we also recorded 6 excavation

attempts in other rose-ringed parakeet populations in Tenerife (Figure 2, Areas III and IV) during the same study period. These populations are isolated from each other and are established in urban areas with similar tree compositions to the study area, but with smaller rose-ringed parakeet populations. Although these excavated cavities were not ultimately occupied by rose-ringed parakeets, the emergence of the same nesting behavior may be an incipient response to the progressive reduction of available cavities by the growing rose-ringed parakeet populations (D. Hernández-Brito, unpublished data). Therefore, this same response may emerge in other rose-ringed parakeet populations, but the spread of these innovative behaviors through the remaining individuals will depend on levels of environmental pressure. Further studies based on marked individuals are needed to delve deeper into differences in behavioral traits among individuals that may promote nesting innovations and their potential cultural transmission during the invasion process of this species.

Despite the benefits associated with increased in resource availability, innovative behaviors, as a form of behavioral flexibility, can entail costs (Snell-Rood 2013). The usurpation of monk parakeet nests could be considered risky due to interspecific aggressions (Grether et al. 2013). Aggressions performed by rose-ringed parakeets can be fatal to the target species (Hernández-Brito et al. 2014b, 2018; Covas et al. 2017). However, we did not record aggressions resulting in death between both parakeet species. Moreover, monk parakeets often show a high tolerance to other species that use their nests (Hernández-Brito et al. 2021a), so negative effects of aggressions are not determinant for innovative rose-ringed parakeets using monk parakeet nests. On the other hand, the excavation of new cavities could be costly expensive in terms of time and energy, so even some primary cavity nesters sometimes reuse tree cavities instead of excavating new ones (Wiebe et al. 2007). However, reuse of nest-site rather than the excavation of new cavities involves risks that may reduce breeding success (Wiebe et al. 2007), such as increased parasite load per breeding season (Johnson 1996), potential detection as a predictable food resource by predators (Nilsson et al. 1991), less tracking of temporal and spatial variability in food resources (Wiebe et al. 2007), and poor microclimate conditions of cavities (Wiebe 2001). Although we were unable to identify whether a same pair occupied an excavated cavity throughout different breeding seasons, the persistence of occupation of these

represents a breeding strategy consolidated in the population, but also can have significant impacts on the recipient community. Thus, rose-ringed parakeets function as an ecosystem engineer (Crooks 2002) by taking the role of primary cavity nesters by providing tree cavities to secondary cavity nesters at a larger scale. Although Yosef et al. (2016) have reported that cavities previously enlarged by rose-ringed parakeets were occupied by native bird species after their abandonment, we did not observe this nesting facilitation in our study population, as other cavity nesters present in the area do not breed in trees (Martín and Lorenzo 2001). Nevertheless, the excavated cavities we recorded in other rose-ringed population in Tenerife, which was not ultimately used by rose-ringed parakeets, were later occupied by feral pigeons (*Columba livia* var. *domestica*) and African blue tits *Cyanistes teneriffae*. Therefore, the facilitation of tree cavities in the study area could assist other species that may not nest in areas without cavities, thus enhancing positive interactions between an invasive species that provides limited resources and native species that exploit them (Rodriguez 2006; Hernández-Brito et al. 2021a).

Rose-ringed parakeets can also occupy chambers within the nests of the invasive monk parakeet when nesting sites are scarce. Although the usurpation of active monk parakeet nests can be considered a form of parasitism, the aggressive behavior of rose-ringed parakeets provides an effective anti-predatory behavior (Hernández-Brito et al. 2014a, 2014b) that secondarily benefits monk parakeets, thus leading to the potential establishment of mutualistic or commensalistic relationships. Therefore, the initial costs to monk parakeets associated with nest losses may be offset for by the cooperative defense against predators (Blanco and Tella 1997; Lima 2009). Predation pressure is an important factor affecting both species (Hernández-Brito et al. 2020; Mori et al.2020), so these positive interactions may increase their likelihood of population growth, and thus their impacts (invasional meltdown; Simberloff and Von Holle 1999).

Impacts of invasive species can emerge over long time scales following the effects of evolutionary processes, such as adaptation to a new environment (Colautti and Lau 2015), the acquisition of a new host, or the development of particular adaptive behaviors (Hernández-Brito et al. 2020, 2021b), as shown here. Therefore, the possibility of unexpected behavioral innovations should be considered in the understanding of biological invasions, as well as for effective prevention and management. In our case, the potential spread of this invasive population outside of the study area not only depends on the transference rate of nesting innovations between individuals but also on the availability of palm trees in the novel areas. Palm tree species are abundant both in urbanized and natural environments in Tenerife, especially the Canary Island date palm with ca. 100,000 specimens on the island and located mainly in urban areas (IDE-Canarias 2018; Sosa et al. 2021). Therefore, management actions on this invasive species (e.g., Esteban 2016; SIF 2017; Bunbury et al. 2019; Saavedra and Medina 2020) must consider its potential further expansion helped by innovation in nesting.

Figure 4 Mean (± 95% confidence interval) entrance size, height above ground and conspecific aggregation of natural nests used, natural nonused, and innovative nests.

cavities together with the fact that there were no significant differences in breeding success suggest that negative effects associated with nest-site reuse are minimal. Moreover, innovative nesting strategies seem to largely compensate for their costs as the number of pairs exhibiting these nesting innovations grows annually.

It has been previously reported that invasive rose-ringed parakeets can enlarge previously available holes or excavate them using tree wounds, even burrowing in the remains of old and dry fronds (Czajka et al. 2011; Orchan et al. 2013; Hernández-Brito et al. 2014a; Yosef et al. 2016). However, the excavation of whole holes in healthy palm trees recorded in our study shows that it can solve the problem of cavity shortage through a highly innovative capacity associated with high nesting plasticity. This innovation not only

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest Statement

The authors declare that all authors have no conflict of interest.

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