‘The early bird catches the nest’: possible competition between scops owls and ring-necked parakeets

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Abstract

Competition for critical resources is one of the key mechanisms through which invasive species impact on native communities. Among birds, the widely introduced ring-necked parakeet Psittacula krameri locally affects cavity-nesting communities through competition for suitable tree cavities, although it remains unclear to what extent such competition translates into population declines of native species. Here, we studied the potential for nest site competition between ring-necked parakeets and the native scops owl Otus scops, a small nocturnal migratory raptor, by comparing the spatial distribution of the nest site locations of the raptor before (2002) and after (2015) the parakeet invasion. Pre-invasion nesting sites of scops owls (2002) strongly coincided with those selected by ring-necked parakeets, but although both parakeet and scops owl populations increased during the study period, this was no longer true for 2015. Ring-necked parakeets took over several cavities formerly occupied by scops owls, and land-use data suggest that because of the higher overall breeding densities in 2015, scops owls were forced to occupy suboptimal breeding habitats to minimize nest site competition with invasive parakeets. Ring-necked parakeets start breeding early in the season, a behaviour enabling them to secure the best nest sites first, before the owls return from their wintering grounds. Our study highlights that locally observed competition not necessarily impacts on population dynamics of competing species and thus warns against uncritical extrapolation of smaller scale studies for assessing invasive species risks at larger spatial scales. Nonetheless, given the increasing number of studies demonstrating its competitive capacities, monitoring of ring-necked parakeet populations is prudent and mitigation measures (such as mounting of man-made nest-boxes, which are used by scops owls, but not by parakeets) may be justified when the parakeets are likely to invade areas harbouring cavity-nesters of conservation concern.

Introduction

The competitive success of an alien species is mediated by its biological attributes (traits), the environmental features of the invaded range and the biotic interactions occurring in the receptive ecosystem (Huenneke & Thomson, 1995; Brown, Mitchell & Graham, 2002; Duncan, Blackburn & Sol, 2003). Competition for limiting resources often represents one of the first interactions between an introduced species and its new environment (Wiens, 1977; Newton, 1994; Villà & Werner, 2004). For instance, grey squirrels Sciurus carolinensis introduced into Europe are more efficient than native red ones Sciurus vulgaris to exploit food resources, enabling them to reach high population densities (Kenward & Holm, 1993; Gurnell, 1996; Chung-MacCoubrey, Hagerman & Kirkpatrick, 1997; Bertolino et al., 2015). Competition with introduced grey squirrels causes weight loss among native red squirrels, consequently reducing their reproductive fitness (Wauters & Dhondt, 1989; Wauters, Tosi & Gurnell, 2002). Among birds, the ring-necked parakeet Psittacula krameri (hereafter, RNP) is a well-known invader globally. Because of its popularity as a pet bird, this gregarious parrot, naturally distributed across much of subtropical Sub-Saharan Africa and large parts of Eastern Asia, has been introduced throughout the world, but especially across Europe (Menchetti, Mori & Angelici, 2016). Although most of Europe is...
considerably colder than the climate conditions RNP's experience across their native range (Strubbe et al., 2015), at least 90 self-sustaining populations are currently established across Europe (Parau et al., 2016). The association of the species with human-modified habitats in its native range (Strubbe et al., 2015) may be the key of its invasion success in anthropic habitats elsewhere (Clergeau & Vergnes, 2011; Holling, 2011; Mori et al., 2013). Impacts of introduced RNP range from competition with native species (e.g. the nuthatch Sitta europaea: Strubbe, Matthysen & Graham, 2009; the starling Sturnus vulgaris: Braun, Czajka & Wink, 2009; Dodge & Battisti, 2014; noctule bats Nyctalus spp.: Hernandez-Brito et al., 2014; Menchetti, Scalera & Mori, 2014; the hoopoe: Yosef, Zduniak & Zmiorski, 2016), to agricultural damage (Menchetti & Mori, 2014) and the transmission of parasites and diseases (Sa et al., 2014; Mori et al., 2015). For reproduction, the RNP largely depends on tree cavities (Khan, Beg & Khan, 2004; Menchetti et al., 2016), which may represent a limiting resource (Cornelius et al., 2008). In its native range, the species is known to readily accept crevices in wall or rocks as nesting sites when tree cavities are in insufficient supply (Lamb, 1996), and such behaviour has been reported from across Europe too (anecdotal observations in Belgium, the Netherlands, Germany, Israel and Italy; pers. obs. of the authors). A plethora of native European species, for example, tits, flycatchers, nuthatches, woodpeckers and bats, also use tree cavities as nesting or roosting sites (Newton, 1994; Hernandez-Brito et al., 2014), which may elicit competition with introduced RNP. RNP are fierce, medium-sized birds (body mass: 120-140 g, Butler et al., 2013), capable of winning aggressive encounters with raptor species such as lesser kestrels Falco naumanni (Hernandez-Brito et al., 2014). In addition, RNP may take advantage of their early breeding phenology (parakeet egg laying can start from half February: Butler et al., 2013), enabling them to occupy the best nesting cavities first (Strubbe & Matthysen, 2009). Displacement behaviour by introduced RNP is particularly concerning when directed against threatened species, for example, native parrots living in oceanic islands or endangered bats (Hernandez-Brito et al., 2014; Menchetti & Mori, 2014). In Europe, RNP have been observed while harassing or displacing native species from breeding sites (birds: Strubbe & Matthysen, 2007; Braun et al., 2009; Strubbe et al., 2009; Czajka, Braun & Wink, 2011; mammals: Hernandez-Brito et al., 2014; Menchetti et al., 2014). In addition, RNP can also enlarge existing tree holes, thereby potentially making cavities unsuitable for smaller cavity-nesters (Orchan et al., 2013). Hernandez-Brito et al. (2014) found that, in urban parks of Seville (Spain), aggressive interspecific interactions and cavity modification by RNP caused a decline in the number of roosting greater noctules Nyctalus lasiopterus, and detected a pattern of mutual spatial segregation between breeding parakeets and the remaining roosting bats. In Italy, Germany and the UK, no relationship was found between breeding densities of parakeets and native starlings (Sturnus vulgaris), yet parakeets were found to occupy the highest tree cavities. This suggests that the competition with parakeets forces starlings to breed in lower cavities, likely increasing nest predation risk by terrestrial predators (DEFRA, 2010; Czajka et al., 2011; Dodaro & Battisti, 2014).

Among hole nesters, the scops owl Otus scops is a small nocturnal migratory raptor (body mass: 64–135 g; Cramp, 1985) which breeds in tree cavities, even if sometimes (e.g. when suitable tree cavities are not available), it may build nests in wall cavities as well (EM, personal observation). In Europe, the species is present during the breeding period only, as most individuals migrate to sub-Saharan Africa for winter, with only few sedentary populations in southern Europe (Mori, Menchetti & Ferretti, 2014; Mori et al., 2016). Scops owls mainly forage in grasslands and ecotones between woodland and open areas, that represent the typical habitats for orthopterans, their main food resource. Scops owls are negatively affected by human-driven landscape modification (Marchesi & Sergio, 2005; Treggiari et al., 2013), as intensification of agriculture reduces the availability of insects, as well as of trees with cavities (Arlettaz, 1990; Sergio, Marchesi & Pedrini, 2009; Treggiari et al., 2013). The species is currently declining throughout its range (Marchesi & Sergio, 2005), despite being classified as ‘Least Concern’ by BirdLife International (2012) on the most recent global and European red lists. In Central Italy, the species often nests in man-made structures close to human settlements (Panzeri, Menchetti & Mori, 2014), probably because tree cavities in these environments represent a limiting resource. As a consequence, competition with introduced RNP may occur. To date, competition between RNP and nocturnal raptors has been poorly studied. In its native range, the RNP is responsible for displacement behaviour against small owl species (e.g. the forest owllet Heteroglaux blewitti: Ishiaq & Rahman, 2005 and the spotted owllet Athene brama: Pande et al., 2007). By contrast, in the introduced range, interactions of RNP with nocturnal raptors are only known from anecdotal observations (e.g. harassment against little owls Athene noctua, Menchetti & Mori, 2014). RNP are non-migratory early breeders (Strubbe & Matthysen, 2009), preferably colonizing areas characterized by edge habitats, thus their ecological requirements at least partially overlap with those of scops owls during the breeding season (Panzeri et al., 2014; Menchetti et al., 2016).

Here, we test the hypothesis that RNP compete for nesting cavities with a nocturnal, cavity-breeding raptor by analysing the spatial distribution of the scops owl nesting sites before and after the invasion by RNP of an urban area in Central Italy. We expect that (a) semi-colonial ring-necked parakeets will exhibit spatial clustering of nest site locations while territorial scops owls should show spatial segregation, (b) if these species compete for nest sites, locations of their breeding sites should show a strong spatial segregation. If competition occurs, reproducing scops owls may be forced to use lower quality areas as breeding territories. Accordingly, we predicted that activity centres of scops owls after RNP invasion (2015) will show lower amounts of potential high-quality foraging habitat (grasslands and edges) than sites occupied before the RNP invasion (2002).
Materials and methods

Fieldwork

The work was carried out within the urban area of Follonica, on the coastal area of Southern Tuscany (Province of Grosseto, Central Italy: 42.92°N, 10.76°E). The study area (about 56.6 km²) is located in the Mediterranean temperate zone at 5 m above sea level, with a mild climate. Mean annual temperature is about 6°C, while annual precipitation is about 650–700 mm. The urban area is surrounded by cultivations (cereals and sunflower mainly) and a wide coastal pinewood Pinus pinea (Lippi et al., 2000). No major changes in the structural, floristic and environmental attributes of the study area occurred during the period of our study, nor are we aware of any significant changes in management practices for the area.

A playback census was performed to assess the number of breeding pairs through the use of two recordings (advertising and alarm calls broadcast one after the other in the same bout) to avoid results being affected by the features of a single recording. Scops owl counts were carried out in summer 2002 and in summer 2015: the same stations were visited once a week throughout the study after dusk, regardless of weather. Researchers stayed for 2 minutes in silence at each station to record spontaneous calls of the target species. Then, a playback was broadcast for 2 minutes and a reaction was waited for further 3 minutes following the protocol by Bibby et al. (2000), but modified by Mori et al. (2014). Broadcast volume was adjusted every time to obtain the clearest vocal rendition possible (Mori et al., 2014). Each response to playback/spontaneous call was noted and recorded on a GPS device. Points were located according to the trees used by scops owls; in some cases, it has not been possible to exactly locate the cavity (i.e. where canopy and leaves covered most of the highest branches). This also prevented us to determine hole availability. A population of RNP is present in the vicinity of Follonica since 1999, when the first two individuals were observed, and no more than three breeding pairs were present in 2002 (Mori et al., 2013). Population size in 2015, obtained through roost counts, is about 30–35 individuals, roosting on plants of Platanus orientalis or Pinus pinea. At the Follonica roost site, counts started 30 min. before sunset and finished 5 min after no more birds came to the roost. Given the relatively small population size, incoming parakeets were counted individually. We discarded movements between roosting trees and subtracted any individuals who left the roost, mostly to return a bit later (Luna et al., 2016). A census of parakeet breeding was carried out through direct observations of parakeets present in the study area. Tree cavities were deemed occupied if parakeets were observed entering the cavity on at least three occasions and/or when a parakeet showing signs of breeding (broken tail feathers, incubation patch) was seen leaving or entering a cavity (Strubbe & Matthysen, 2009).

Statistical analyses

The spatial (geographical) location of RNP and scops owl breeding cavities can be analysed as a spatial point pattern (Baddeley et al., 2006). Spatial point pattern analyses model interactions through the use of an intensity function, whereby the probability of establishment of other breeding pairs is increased (aggregated, clustered, overdispersed) or decreased (regular, underdispersed), and/or a zone from which other pairs are totally excluded. The method can be used to test for patterns of spatial competitive exclusion by comparing the observed spatial pattern against a hypothesized spatial process model assuming no interaction exists between study species. Examples include its use to detect competition between ant species by assessing the locations of their nests (Harkness & Isham, 1983), to study interspecific competition among goose species breeding in the Arctic (Reiter & Andersen, 2013) and the spatial arrangement of barnacles across intertidal surfaces (Hooper & Eichhorn, 2016). To verify whether the assumption of stationarity (‘spatial homogeneity’, i.e. the probability of observing some point pattern at a specific location is independent of the location), we first applied a kernel-smoothed intensity estimate for the breeding locations of each species, and then plotted the ratio of owl and RNP smoothed intensity estimates to visually assess spatial trends in this ratio (Baddeley et al., 2006). As this plotted ratio was largely constant across the study area, data can be considered to be spatially homogeneous. We proceeded with fitting a multitype hard-core Strauss model to our datasets. This model employs two components, namely a ‘hard core distance’ which represents a total exclusion zone around a breeding cavity, and an ‘interaction radius’ in which the probability of finding further nests is in-or decreased (Baddeley et al., 2006; Blanco-Moreno et al., 2014).

Hard-core distances were estimated from the data using minimum inter-point distances (i.e. minimum distances between scops owl nests, between RNP nests and between scops owl and RNP nests: Baddeley et al., 2006). These distances were estimated at 59–62 m for scops owl (in 2002 and 2015 respectively) and at 0.76 m for RNP (2015). The between-species hard-core distance was 42 m (in 2015). To test for changes in scops owl spatial nest distribution since the colonization of the park by RNP, we superimposed the 2015 RNP nest locations on the 2002 scops owl breeding distribution, resulting in a 0.12 m hard-core distance for the superimposed 2002–2015 owl-parakeet data. Interaction radii were estimated based on the species ecology. While the average home range of breeding scops owl can be approximated by a circle with a radius of about 300 m (Martínez et al., 2007), the species is known to respond to the presence of congeners over longer distances (Galeotti, Sacchi & Perani, 1997). Scops owl calls can be heard from a distance of c. 800 m (E.M. pers. obs.) and we therefore selected this distance as an upper limit for the scops owl interaction radius. By contrast, RNPs are not territorial and often nest in loose, semi-colonial groups. When a predator is noticed, RNPs often engage in frantic mobbing behaviour, drawing neighbouring parakeets from a distance up to c. 150 m (all
authors, personal observation). Consequently, RNP–RNP and RNP–scops owl interaction radii were set at 150 m. Spatial point pattern analyses output an interaction parameter \( c \), whereby \( c < 1 \) indicates inhibition between species and \( c > 1 \) point to attraction between species. We first assessed within-species interaction (scops owl in 2002 and in 2015, RNP in 2015), and then tested for between-species interactions (scops owl vs. RNP in 2015). Significance of within and between-species interaction estimates was tested by means of 249 Monte Carlo simulations of the null model and refitting the null and the alternative models (Blanco-Moreno et al., 2014). All analyses were carried out using the R package ‘spatstat’ (Baddeley, Rubak & Turner, 2015).

In order to quantify scops owl breeding habitat quality before and after the parakeet invasion, land use and land cover was obtained by photointerpretation of satellite images (scale 1:25 000). We extracted the amount of grassland and edge habitat present within a 300 m radius (known home range of breeding scops owls: Martínez et al., 2007) as a proxy for available hunting grounds, and thus breeding habitat quality. Pre- and post-invasion measures of scops owl habitat quality were then assessed using linear models specifying year as a fixed effect. Assumptions of normality and homoscedasticity of residuals were met (Shapiro-Wilk \( W > 0.90 \)). It should be noted that from 2002 to 2015, breeding scops owl increased from 12 to 16 territories and that any decrease in average habitat quality could thus be due to intraspecific competition. For a stricter test of parakeet impacts, we therefore performed an additional analysis in which we considered only the 12 highest quality scops owl territories of 2015 (i.e. those 12 territories with the highest amounts of grassland and edge habitat). Spatial analyses were conducted in QGIS 1.6. Differences were considered significant when \( P < 0.05 \). XLSTAT (Addinsoft) was used for statistical analyses.

**Results**

In 2002, field censuses detected 12 breeding couples of scops owls, while in 2015, 16 scops owl nests and eight RNP nests were found. Direct, aggressive interactions between the species have never been observed, yet, but at least five cavities used by scops owl in 2002 were taken over by RNPs in 2015 (Fig. 1). There was no convincing evidence for within-species interactions among scops owls. In 2002, the interaction estimate \( \gamma \) was 1.16 (indicating mild attraction), whereas in 2015, it was 0.91 (suggesting mild inhibition), but both these estimates failed to reach statistical significance (\( P = 0.16 \) and \( P = 0.23 \) respectively). By contrast, RNPs showed strong intraspecific attraction (\( \gamma = 3.60, P < 0.01 \)). The 2015 data are suggestive of mild inhibition between scops owl and RNP (\( \gamma = 0.88 \)), but data do not allow strong conclusions as the associated \( P \)-value is 0.15. Yet, when superimposing the 2002 scops owl data onto the 2015 RNP nest distribution, we found strong attraction between these two cavity-nesters (\( \gamma = 2.98, P < 0.01 \)). Compared to the year 2002, in 2015, scops owl nests were characterized by significantly lower amounts of

![Figure 1](image-url)
discussion

although both the number of breeding scops owls and parakeets increased over the course of our study, spatial patterns in nest site choice nevertheless suggest that competitive interactions take place between these obligate cavity-nesters. our attraction–inhibition analysis indicated that pre-invasion nesting sites of scops owls strongly coincide with those of RNP (post-invasion). After the invasion by RNPs, this is no longer true, indirectly pointing to an impact of RNP on the spatial distribution of scops owl breeding distributions. We did not observe any direct aggressive interaction or nest displacement of scops owls by invasive RNPs, but our data clearly showed that, if in 2015 owls were to be found at the same breeding sites as in 2002, a strong positive association between spatial distribution of these species would have been apparent. The fact that such a spatial association was not detected in 2015 suggests that RNPs and scops owl compete for nesting cavities. Indeed, at least five cavities formerly occupied by scops owl in 2002 were taken over by parakeets in 2015, leading to a marked decrease in scops owl numbers (from five to one breeding pair only) in the Ex Ilva park (a 10.35 ha large park at the centre of our study area), where the bulk of the parakeet population currently breeds (at least six pairs in 2015). All tree cavities used by scops owls in 2002 were still present in 2015, and apart from the five cavities taken over by the parakeets, all other nesting cavities used by scops owl in 2002 were used by owls in 2015 as well. No other major changes occurred within our study area between 2002 and 2015, corroborating our interpretation of competition as main driver of the changes observed.

strubbe et al. (2009) found that due to their early breeding phenology (first eggs can be laid by half February: Butler et al., 2013), RNPs have a competitive advantage over native cavity-breeders, enabling them to occupy high-quality nesting cavities first. This mechanism may have occurred in this case as well. RNPs have been observed entering and occupying multiple cavities previously used by scops owls, forcing the owls to search for other, potentially suboptimal nesting sites when they return from their wintering grounds. Indeed, scops owl are known to prefer to breed in edge habitats surrounded by wide grasslands (Panzeri et al., 2014), as such habitats represent good foraging areas (Latková, Sándor & Krištín, 2012). A comparison of the amount of grassland surrounding scops owl nests in 2002 versus 2015 showed that, in the latter year, scops owl territories contained significantly less grassland and edge habitats. This could be partly due to the fact that higher intraspecific competition (from 12 breeding pairs in 2002 to 16 in 2015) forced scops owls to occupy suboptimal sites. However, even when considering only the 12 “best” scops owl territories of 2015 (i.e. those with the highest amount of grassland and edge habitats), these still included less grassland and edges than the pre-invasion territories.

In its native Asian range, RNPs are known to compete with nocturnal raptors comparable to scops owls in terms of body size and ecology (Ishtiaq & Rahmani, 2005; Pande et al., 2007) and it is thus not surprising that such nest site competition also takes place in invaded Europe. Yet, while there is increasing evidence for local competition between parakeets and a variety of native species that depend on tree cavities, it remains unclear whether and how such local impacts translate into detrimental effects upon population dynamics of native species at large spatial scales.

Current invasive species risk assessment schemes advise to search the literature for any impact documented and rank invasive species according to their worst documented impact (Evans, Kumschick & Blackburn, 2016). Our study may suggest that such an approach overestimate invasive species impacts, as while we can reasonably argue that ring-necked parakeets are able to locally displace native scops owls, this does not translate into regional population declines – on the contrary in this case. Similarly, in Brussels, Belgium, Strubbe & Matthysen (2007) found that while native nuthatches Sitta europaea were less abundant than expected in areas with higher parakeet densities, longer term population monitoring trends derived from point counts suggested a fluctuating but overall stable trend in nuthatch abundance. Nonetheless, given the general lack of autecological studies on invasive species impacts (Strubbe, Shwartz & Chiron, 2011), any evidence of interactions between native and invasive species constitutes crucial information to prioritize conservation actions and control efforts (Ruscoe et al., 2011; Orchan et al., 2013). The RNP is one of the most successful avian invaders in Europe in general and in the Mediterranean basin specifically (Menchetti et al., 2016). This study adds to the growing body of evidence that RNP can, at least locally, impact native species breeding behaviour. A recent review of RNP population growth trends showed that there are many, fast-growing RNP populations across the Mediterranean (Páirau et al., 2016). Accordingly, statistical models of invasion risk (Di Febbraro & Mori, 2015; Strubbe et al., 2015) indicate that across the Mediterranean, there is ample suitable habitat available for RNPs to spread into. Moreover, differently from the parakeet populations in the coldest parts of Europe, the species may be able to spread outside of the urban strongholds where the bulk of the populations currently reside (Strubbe et al., 2015). Therefore, especially in the Mediterranean, monitoring of RNP distributions and population trends is prudently required. In case RNPs are likely to invade areas where cavity-nesters of conservation concern are present, mitigation measures such as providing man-made nest-boxes (allowing entrance by scops owls, but excluding parakeets: Lambrechts et al., 2012) or trapping/numerical control of parakeets (Genovesi & Shine, 2004) may have to be considered.
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