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What can the abundance of Grey Parrots on Príncipe Island tell us about large parrot conservation?

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Abstract

While populations of the Endangered Grey Parrot *Psittacus erithacus* have collapsed across its range, the species remains remarkably abundant on the island of Príncipe, Gulf of Guinea. We examine how aspects of its ecology interplay with local environmental conditions, to inform conservation strategies for this species and other large parrots. On Príncipe, parrots breed in large trees of common species, with nest densities (42 ± 34 km^{-2}) greatly exceeding those for any comparably sized parrot. Productivity is high (1.9 chicks per cavity), probably reflecting the absence of nest competitors and predators. Food sources are abundant and much of the island is inaccessible to trappers, so many nests are successful each year. Historically harvest has involved taking only chicks from trees in a few traditional patches. These conditions have combined to allow Grey Parrots to thrive on Príncipe, while elsewhere nest trees are timber targets, nest competition and nest predation are likely to be more intense, trapping is indiscriminate, and few areas remain unexploited by trappers. Preservation of large trees as breeding refugia, and vigilance against the indiscriminate trapping of adult birds, are identified as key conditions to stabilize and recover mainland Grey Parrot populations and indeed large parrots generally, given their very similar ecological traits and anthropogenic circumstances.

Introduction

Parrots (Psittaciformes) are among the most imperilled bird orders, with 28% of species currently Threatened and 24% Near Threatened (BirdLife International 2020*a*), with large species being three times more likely at risk than small ones (Collar 1998). Most parrot species are threatened by a combination of habitat loss or degradation and excessive trade (Snyder *et al.* 2000, BirdLife International 2020*a*). Grey Parrot *Psittacus erithacus* has a huge range in West and Central Africa, but populations have been subjected to intense anthropogenic pressures (BirdLife International 2020*b*). Over the last 30 years the species' habitat has been disappearing at increasing speed (Achard *et al.* 2002, Duveiller *et al.* 2008), and tens of thousands of individuals have been harvested from the wild to satisfy a multi-million dollar international pet trade (Martin 2017, UNEP-CITES 2017). The species' global conservation status rapidly deteriorated from Near Threatened through Vulnerable to Endangered in just five years (BirdLife International 2020*b*), resulting in a near-unanimous acceptance of calls for a ban on its international trade in 2016 (CITES 2017).

Population trends in the Grey Parrot have not been geographically uniform: its status ranges from reasonably common in parts of Cameroon (Fotso 1998, Marsden *et al.* 2016) to declining in DRC (Hart *et al.* 2016) and Côte d'Ivoire (Marsden *et al.* 2016), to almost extinct in Ghana (Annorbah *et al.* 2016) and Nigeria (Martin *et al.* 2014, Olmos & Turshak 2009). However, despite a long history of commercial trade in Grey Parrots, the island of Príncipe (Democratic Republic of São Tomé and Príncipe) still hosts an abundant population (Valle *et al.* 2018), with a remarkably high overall mean density of 53 ± 6 parrots km^{-2} across the island (Valle *et al.* 2017). Although the Grey Parrots on Príncipe present some genetic complexity, with one lineage involving *Psittacus erithacus* and one involving Timneh Parrot *P. timneh* (Melo & O'Ryan 2007), there is no evidence that their ecology is significantly different from populations of either species on the African mainland.

In this paper we seek to explore the various factors that might individually or in combination explain why the Grey Parrot population on Príncipe maintains such notable densities while other populations are dwindling.

Methods

Study area

Príncipe (139 km^2) lies close to the equator, 220 km off the coast of West Africa, in the Gulf of Guinea (Supplementary online material figure S1). It was uninhabited until 1471, after which all sufficiently accessible areas were gradually cleared and planted with sugarcane *Saccharum* sp., oil palm *Elaeis guineensis*, cocoa *Theobroma cacao*, coffee *Coffea* sp. and coconut *Cocos nucifera*. Many of these areas have now reverted to secondary forest, while, from our own calculations using GIS, ~25% of the island (mostly in the southern half) retains almost untouched lowland rainforest (Figueiredo *et al.* 2011, Jones & Tye 2006). Príncipe has a depauperate land fauna, with only 31 breeding bird species (Jones & Tye 2006), 11 reptiles and three amphibians (Ceríaco *et al.* 2018), and five native mammal species (four bats and one shrew), albeit with high levels of endemism (Jones 1994).

Review

We reviewed all available evidence concerning those factors which are known to be key to the viability of parrot populations. These include natural ecological aspects as well as indirect and direct anthropogenic pressure. Availability of suitable nesting cavities is a key factor for most parrot species as it imposes a direct limitation on their yearly breeding output (Beissinger 2001, Beissinger & Bucher 1992, Munn 1992). Natural nest predation is another important aspect as it can be accountable for more than 50% of nest failures in some populations (Berkunsky *et al.* 2016, Renton & Salinas-Melgoza 2004). Changes in food resource availability and accessibility have also been linked to the decline of wild parrots (Berg *et al.* 2007, Saunders 1990, Wunderle 1999). Furthermore, as most Psittacidae rely on tropical and subtropical forests, habitat loss has been highlighted as one of the main threats at both local and global levels, particularly when associated with agricultural expansion (Koenig 2008, Vergara-Tabares *et al.* 2020). Finally, harvest for the local and international pet trade is thought to be responsible for the decline of many parrot species due to their peculiar life history traits, i.e. small clutch size, long period of parental care, slow sexual maturation and long lifespan (González 2003, Martin *et al.* 2014, 2018, Valle *et al.* 2018). We then examined how the same conditions may differ in mainland Africa and how this may influence the health of populations of this and other large parrot species.

Results

Nesting requirements, densities and productivity

Grey Parrots are obligate secondary tree-cavity nesters (Benson *et al.* 1988), which makes them particularly sensitive to the loss of suitable cavities to tree-felling or competition (Valle *et al.* 2017). On Príncipe, 66 of 83 (79%) nest cavities examined were found in four relatively common and widespread tree species (Valle 2015; Supplementary online material table S1). Pairs nested in large trees (mean nest-tree height ± SD = 45.3 ± 14.0 m; DBH = 1.22 ± 0.49 m), and all but four nests were in living healthy trees (Valle 2015). This is consistent with the species' behaviour elsewhere (Amuno *et al.* 2010, Dändliker 1992) and indeed with larger parrot species across the tropics (Marsden & Jones 1997, Monterrubio-Rico *et al.* 2006).

Although the loss of habitat in general is a major threat to Grey Parrot populations (BirdLife International 2020*b*), the loss of individual large trees providing nesting substrate can be equally detrimental to their viability (Valle *et al.* 2017). In some cases, preferred nest trees may be of significant commercial value, e.g. *Terminalia superba* for timber in Ghana (Dändliker 1992) and *Pentaclethra macrophylla* for charcoal in Príncipe (Valle 2015). Indeed, in Ghana, the felling of individual large trees within the landscape is thought to have greatly compounded the effects of trade in the species (Annorbah *et al.* 2016).

Nest densities at traditional trapping sites on Príncipe averaged 72 ± 26 (SD) nests km^{-2} in primary forest and 17 ± 8 nests km^{-2} in secondary forest (Valle 2015). While nest densities across the island as a whole may be lower than those at selected trapping sites, they are nonetheless the highest ever recorded for any native, non-colonial, tree-nesting parrot species (Table 1). The only other estimate of nest density for Grey Parrots is 1.3 ± 0.13 (SD) nests km^{-2} in Nigeria (as in this study, minimum density was calculated from local trappers' knowledge; McGowan 2001).

On Príncipe, nests were reported by trappers to have produced 1–3 chicks (mean ± SD = 1.9 ± 0.7, n = 81; Valle 2015). Such productivity is high but within the normal range of the species (1–4; Benson *et al.* 1988, Forshaw 1989).

Nest competitors and nest predators

On Príncipe, Grey Parrot is the largest hole-nesting vertebrate (Jones & Tye 2006), freeing it from interspecific competition for cavities, a limiting factor for many bird species (Martin & Eadie 1999, Strubbe & Matthysen 2009). The absence of hornbills (Bucerotidae) may be particularly important, since these are the most likely nest-site competitors across the Grey Parrot's range, and because they can occur at relatively high densities, e.g. Black-casqued Hornbills *Ceratogymna atrata* at 8.7 ± 0.6 km^{-2} and Brown-cheeked Hornbills *Bycanistes cylindricus* at 7.2 ± 1 km^{-2} in Cameroon (Whitney & Smith 1998). Indeed, the only documented instance of nest competition on a Grey Parrot involved a Grey-cheeked Hornbill *B. subcylindricus* killing a brood in order to appropriate the cavity (Kalina 1988). Also absent from Príncipe is a suite of tree-dwelling mammals (e.g. Galagidae, Viverridae, Mustelidae), which may likewise compete for nest holes in mainland West and Central Africa.

Other than the introduced mona monkey *Cercopithecus mona* and black rat *Rattus rattus*, which may despoil unguarded nests (Jones & Tye 2006), there are no confirmed nest predators on Príncipe (Dutton 1994). Nest predation can seriously affect productivity and density in parrots (Britt *et al.* 2014), and in mainland Africa the same mustelids and viverrids that compete for cavities may also be predators on hole-nesting animals, as are various arboreal primates and snakes, e.g. Patas monkey *Erythrocebus patas* (Hall 1965) and royal python *Python regius* (Luiselli & Angelici 1998).

Food resources

Grey Parrots feed on fruits and seeds from a variety of common species, with a marked preference for oil palm fruits (Benson *et al.* 1988, Brosset & Erard 1986), and 17 known 'food tree species' (Chapman *et al.* 1993, Dändliker 1992, Juste 1996, Tamungang & Ajayi 2003). This diet allows the species to occupy a range of disturbed habitats, including secondary forest (Dändliker 1992), shade plantations (Valle *et al.* 2017) and even urban environments (Irumba *et al.* 2016, Martin *et al.* 2014). Príncipe's landscapes are rich in Grey Parrot food, with a mean 4 ± 2 (SD) of the 17 known food tree species per sampling plot

Table 1. Nest densities (nests km^{-2}) for parrot species in previously published studies and the current study, in ascending order. NB. Caution needs to be taken in comparing the figures as methods used to calculate densities vary.

Species	Location	Density ± SD (range)	Habitat type	Reference	Methods/notes
Hyacinth Macaw *Anodorhynchus hyacinthinus*	Pantanal, Brazil	0.045	Savanna, forest patches, flood plains	Pinho & Nogueira (2003)	Methods not described
Blue-fronted Amazon *Amazona aestiva*	Pantanal, Brazil	0.26 ± 0.3 (0.03–0.5)	Savanna, forest patches flood plains	Fernandes Seixas & Mourão (2002)	Active nests located by following individuals to nests and information from trappers
Grey Parrot *Psittacus erithacus*	Nigeria	1.3 ± 0.13 (0.5–2.1)	Various	McGowan (2001)	Calculated from local trappers' knowledge. Minimum nest density
Scarlet Macaw *Ara macao* Blue-and-yellow Macaw *Ara ararauna* Green-winged Macaw *Ara chloroptera*	Manu NP, Peru	6.1	Rain forest	Nycander *et al.* (1995)	Nest/cavity search. Density calculated across all species through extrapolation
Grey Parrot *Psittacus erithacus*	Príncipe	41.5 ± 33.9 (8.8–101.0)	Lowland rain forest	This study	Calculated from local trappers' knowledge. Minimum nest density

(n = 103), 99% containing at least one such species and 89% containing oil palms (Valle *et al.* 2017). As with other parrot species (Marsden & Pilgrim 2003), such adaptability contributes to the species' resilience to some anthropogenic land-use changes. Thus, habitat loss is more likely to affect populations of Grey Parrot, and other large psittacids, in terms of lower nest-site availability than lower food availability (Beissinger & Bucher 1992, Munn 1992, Newton 1994).

Trade volume, patterns and limitations

With over 1.6 million individuals legally exported from range states between 1975 and 2014, Grey Parrot was then the most traded wild bird species in the world (Martin 2017, UNEP-CITES 2017). Despite this, the supply of birds remained strong until growing concerns over the state of wild populations led to a ban on its trade in 2016 (CITES 2017). Príncipe has a history of heavy trade in Grey Parrots, with a reported average of 600 chicks – approximating to four individuals per km^2 of its land area – exported annually in the 1990s (Juste 1996). Nonetheless, the island appears always to have hosted reasonably high densities (Jones & Tye 2006, Melo & O'Ryan 2007), which have been slowly growing since the regional ban on all trade was put in place in 2005 (Valle 2015, Valle *et al.* 2018). We suggest two reasons behind this resilience to trapping pressure.

First, different capture methods have markedly different impacts on Grey Parrot populations, with the harvest of adult birds being far more detrimental than that of nestlings only (Valle *et al.* 2018). Trapping on Príncipe has predominantly targeted chicks from nests in traditional harvest locations, with only occasional trapping at feeding sites (Melo 1998). By contrast, trapping in mainland Africa commonly involves the indiscriminate mass capture of individuals from aggregation sites (e.g. in Cameroon; Ngenyi 2002, 2003) or the capture of nest-attending adults along with destruction of the nest and/or felling of the nest tree (e.g. in Ghana; Dändliker 1992).

Second, at least 45% of Príncipe is covered by practically inaccessible primary and secondary lowland forest (Jones & Tye 2006). This has provided parrots with an abundance of large trees suitable for nesting, a high proportion of which remain beyond the reach of poachers and other forms of disturbance due to their remoteness and the ruggedness of the terrain. This is consistent with what has been found in the congeneric Timneh Parrot, where site remoteness is linked to healthier local populations (Lopes *et al.* 2019). Given these conditions, together with the absence of nest competitors and predators discussed above, it is likely that, on Príncipe, many pairs of Grey Parrots, which are annual breeders (Benson *et al.* 1988), fledge offspring successfully every year. Moreover, the peculiar configuration of the island's landscape might be particularly favourable for Grey Parrots, as it offers areas with significant feeding opportunities (extensive plantations and secondary forest, both rich in food tree species) as well as much rugged forest suitable for breeding, allowing for daily and seasonal movements between the two (Valle 2015, Valle *et al.* 2017).

Discussion

While mainland African populations of Grey Parrot, and indeed most other large parrots worldwide, have been steadily declining (BirdLife International 2020*a*), over the years Príncipe's population has remained relatively large and seemingly growing (Valle *et al.* 2018). Príncipe's high population densities of parrots may be partly attributed to an island 'density compensation' effect (MacArthur *et al.* 1972, Wright 1980). Mainland populations also have to contend with a number of potential predators (including human) and competitors which are absent from the island (Kalina 1988). Nevertheless, some important lessons can be drawn from this case study to inform the conservation of the species elsewhere in its range. Of the four constraints potentially operating on Grey Parrot populations across Africa and which may contribute to the success of the species on Príncipe, we discount one, food resources, as improbable, but we regard the other three as significant. Although the availability of food is an unlikely constraint for Grey Parrots on Príncipe, and possibly in other lush habitats on the mainland, it should not be underestimated as it has been shown to influence local abundance (Marsden & Pilgrim 2003) and limit population viability in other large parrot species (Saunders 1990, Berg *et al.* 2007).

Consequently, we recommend the following management interventions for mainland populations of Grey Parrots and other large psittacines, particularly those with very specific nesting requirements such as Thick-billed Parrot *Rhynchopsitta pachyrhyncha* (Monterrubio *et al.* 2002) and Yellow-eared Parrot *Ognorhynchus icterotis* (Krabbe 2000).

1. Efforts are needed to ensure that a proportion of Grey Parrot nests are successful each year, thereby promoting recruitment into the wild population. Protection of nests, mainly from poachers but also, in some situations, from competitors or predators (e.g. by installation of predator guard devices), is crucial.
2. The preservation of individual large trees, especially those known to hold nest holes, is vital, which may require adjustments to forestry policy and negotiations with logging stakeholders.
3. As authorities enforce the international ban on trade, they should prioritize interventions against the indiscriminate trapping of adult birds away from nests. For example, since the eyes of adult Grey Parrots are pale while those of juveniles are dark (Dändliker 1992), the trapping method employed could be deduced by recording eye colour of birds in confiscated shipments, i.e. those with >20% of birds with pale eyes are likely to derive from indiscriminate trapping (Valle *et al.* 2018).

Conservation action for any species is best informed by extensive research into that species in the particular area of concern. However, the logistic and economic constraints of collecting ecological data in the tropics on large parrots indicate the need for a critical synthesis of available evidence, even from just one species, in order to provide information with a high probability of relevance to other species. Such extrapolation should nevertheless be weighed against the possibility of collecting better evidence, and allow for the assessment of the effects of any conservation intervention put in place based on surrogate species.

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