Long-term persistence of conservation-reliant species: challenges and opportunities

Highlights

- Artificial nests are increasing Lesser Kestrel and European Roller populations in Portugal
- All semi-natural nests are expected to disappear by the end of this century
- Lesser Kestrels and Rollers will become fully reliant on artificially provided nests
- Nest provisioning to sustain current populations would require 4500€ every year
- These costs are less than 1% of the region's tourism annual lodging income

Abstract

"Conservation-reliant species" – those fully dependent on continued management actions – are booming and, with limited conservation budgets, securing funds to sustain their long-term viability is becoming overwhelming. This study assesses the degree of dependence on conservation actions of two obligatory cavity-nesters, the Lesser Kestrel *Falco naumanni* and the European Roller *Coracias garrulus*, whose populations in Europe were recently recovered through artificial nest-site provisioning. Using long-term monitoring data and population surveys conducted in their main Portuguese stronghold, we examined temporal changes in the availability and use of semi-natural (cavities in rural abandoned buildings) and artificial nest-sites. We further assessed the financial costs of nest-site provisioning and evaluated the potential use of tourism revenues as a conservation funding source. Following the implementation of conservation projects, the Lesser Kestrel and Roller populations have been increasing but more than 65% of all breeding pairs currently nest in artificial nest-sites. Semi-natural nest-sites remain suitable for approximately 30 years and are expected to disappear by the end of this century. Lesser Kestrels and Rollers will thus become fully dependent on artificial nest-sites and sustaining their current population sizes is estimated to cost 4500€ per year. This represents less than 1% of the region's lodging income, largely supported by nature-based tourism. Our findings suggest that reactive conservation measures can be very effective at recovering endangered populations but can make them fully reliant on the perpetuation of those measures. This demands long-term funding, which can be alleviated by tourism revenues in areas with high nature capital values.

Keywords: European Roller, Lesser Kestrel, Conservation, Artificial nests, Tourism, Funding

1. Introduction

Human activities are transforming the face of the planet and causing dramatic changes to the distribution and abundance of wildlife species, mainly through habitat destruction and climate change (Pimm & Raven, 2000; Sala et al., 2000). The decline of biodiversity detrimentally impacts ecosystems and the services they provide which are essential to humans (MA, 2005; Barnosky et al., 2017; Butchart et al., 2010; Cardinale et al., 2012). Increased recognition of the magnitude of human-mediated impacts on nature has prompted large-scale conservation efforts aiming at halting and reversing ongoing biodiversity loss, often incurring high financial costs (e.g. USD 6 billion/year to manage protected areas; Butchart et al., 2006; James et al., 2001). Although conservation actions help prevent extinctions and improve population trends (Butchart et al., 2006; Hoffman et al., 2010; Rodrigues, 2006), funds available are usually insufficient to offset the major drivers of extinction risk (Hoffman et al., 2010; Sebastián-González et al., 2011; Watson et al., 2014).

Often priority is given to species and populations that are already highly endangered, focusing on reversing negative impacts in the short term (Cardador et al., 2015; Drechsler et al., 2011). Therefore, conservation approaches are often reactive rather than proactive. Generally, funding is constrained in time, limited to the duration of specific programs and/or achievement of successful results, and is then allocated to new conservation priorities (Scott et al., 2010). In the long-term, reactive conservation may be more expensive than a proactive approach (Drechsler et al., 2011) and can lead to conservation traps by promoting an unsustainable need to perpetuate the implementation of active conservation actions (Cardador et al., 2015). The number of "conservation-reliant species" – those requiring continued, long-term management actions and investment – is likely to increase, stretching even further the limited conservation budgets. Hence, cost-efficient actions that guarantee the economically sustainable conservation of threatened populations are urgently needed (Scott et al., 2010; Sebastián-González et al., 2011).

Conservation reliance may be particularly prevalent in human-dominated landscapes, where species have adapted to traditional human activities which have changed dramatically during the last century, the prime example being agriculture intensification (Green et al., 2005; Tilman et al., 2011). As a consequence of these changes, agricultural areas hold many endangered species, and birds associated with farmlands are among those declining the most (Fischer et al., 2010; Socolar et al., 2019; Sodhi et al., 2010; Stanton et al., 2018; Traba & Morales, 2019). Agricultural and other human-dominated landscapes therefore have high levels of biodiversity, often establishing a strong natural and cultural heritage with high aesthetics, ecological and recreational values (Hartel et al., 2014; Schulp et al., 2019).

In areas with high biodiversity or recreational values, conservation programmes can be maintained by the financial income generated by tourism (Steven et al., 2013; Walpole & Leader-Williams, 2002). Nature-based tourism, especially when paired with easy-to-see and charismatic species, has great potential to raise funds and awareness for conservation (Czajkowski et al., 2014; Steven et al., 2013; Walpole & Leader-Williams, 2002). Revenues can be raised from accommodation, donations or nature-related activities such as birdwatching. Worldwide, avitourism is a rapidly expanding subsector of the tourism industry and may foster sustainable tourism and nature conservation by reducing the need for external (e.g. governmental) funding (Czajkowski et al., 2014; Kiss, 2004; Steven et al., 2013).

The Lesser Kestrel (*Falco naumanni*) and the European Roller (*Coracias garrulus*, hereafter Roller) are two charismatic bird species and icons of nature conservation. Both species suffered major population declines in their European breeding ranges (ca. 46% in each decade since 1950s for Lesser Kestrels; 4-20% over three generations for Rollers) and were classified as "Vulnerable" and "Near Threatened, respectively, during the first decade of the twenty-first century (BirdLife International, 2019). The observed declines triggered an increase in conservation efforts that contributed to remarkable recoveries in many European countries, with both species being downlisted to “Least Concern” (although some national populations are still declining; Bux et al., 2008; Catry et al., 2009; Finch et al., 2018; Kovacs et al., 2008; Rodríguez et al., 2011; BirdLife International, 2019).

Like many bird populations in human-dominated landscapes, Lesser Kestrels and Rollers are limited by lack of suitable foraging and nesting resources and conservation strategies have focused on promoting environmentally friendly habitat management and nest-site provisioning (Catry et al., 2013; Finch et al., 2018; Franco et al., 2005; Newton, 1998; Rodríguez et al., 2011). Being secondary cavity nesters, they are unable to excavate their own cavities and are thus particularly vulnerable to shortage of nest-sites. Compelling evidence has been found for the effectiveness of nest-site provisioning as a reactive conservation tool to increase population numbers of many endangered species (Lambrechts et al., 2010; Mainwaring, 2011; Newton, 1994; Sutherland et al., 2018). Whilst the quick success of artificial nest-site provisioning enabled the fast recovery of Lesser Kestrel and Roller populations throughout Europe, the long-term costs of increased dependency of conservation actions, essential for the persistence of these species, has never been evaluated.

In this study we assess the degree of dependence Lesser Kestrels and Rollers have on conservation actions and discuss evidence-based perspectives for their long-term conservation. Using long-term monitoring data, we estimate population trends of Portuguese Lesser Kestrels and Rollers, quantify their dependence on artificial nest-sites and understand temporal changes in the availability of semi-natural ones (cavities in rural abandoned buildings). We then calculate conservation costs associated with artificial nest-site provisioning and compare them with tourism revenues for the region. We aim at illustrating the potential challenges of relying on reactive approaches that may lead to conservation-reliant species, but also the opportunities that arise from tourism to create self-sustainable conservation strategies.

2. Methods

2.1 Study area and species

We focused our study in the Castro Verde Special Protection Area (SPA), located in southern Portugal (37°43′N, 7°57′W). With a total area of ca. 85 000 hectares, it is an important SPA for steppe birds at the European level and one of the main strongholds for several threatened farmland bird species in Western Europe (Moreira et al., 2007). Land use within the SPA has remained relatively stable in the last decades, in part due to the implementation of agri-environmental policy schemes and funding mechanisms that ensure high-quality foraging habitat for many farmland birds (Catry et al., 2013; Silva et al., 2018). This area harbours roughly 80% of the national breeding populations of Lesser Kestrels (418-436 pairs in 2007; Catry et al., 2009) and Rollers (52-55 pairs in 2009; Catry et al., 2011b), where both species have recently reversed declining population trends after the implementation of conservation programs (Catry et al., 2009; Catry et al., 2011b). Together with other key bird species (e.g. Great Bustard (*Otis tarda*), Little Bustard (*Tetrax tetrax*), Black-bellied Sandgrouse (*Pterocles orientalis*), Iberian Imperial Eagle (*Aquila adalberti*)), Lesser Kestrels and Rollers are significant contributors to birdwatching and nature-related activities in the region.

Lesser Kestrels and Rollers are long-distance Afro-Palearctic migratory species (BirdLife International, 2019) and opportunistic cavity nesters. The Lesser Kestrel – a cliff-nesting colonial raptor, benefited from the human occupancy of the landscape, both for foraging and breeding, nesting in isolated farmhouses or castles and churches in villages or towns and feeding on invertebrates in farmland areas (Catry et al., 2009). Rollers are solitary breeders, nesting in woodpecker cavities in trees or sandy banks, but can also occupy human buildings in southern latitudes, mainly where trees are lacking (Rodríguez et al., 2011). Most of the population of both species in the study area (around 300-400 and 40-50 breeding pairs of Lesser Kestrels and Rollers, respectively) have been annually monitored since 2000 by the authors and long-term demographic information (number of nests, eggs, chicks) is available.

2.1.1 Semi-natural and artificial nest-sites

In the Castro Verde SPA, there are no records of birds breeding in the original natural nests (burrows in cliffs or hollows in trees). First known settlers nested in abandoned rural buildings (such as houses or farm sheds), traditionally built with adobe (a mixture of lime and mud) and Arabic tiles. After abandonment or lack of maintenance, these buildings decay due to the eroding action of wind and rain, leading to the formation of cavities in walls or under roof tiles, opportunistically used by both species to breed. Because these cavities are not true natural nests, we hereafter refer to them as semi-natural nest-sites. Contrarily to traditional buildings (built at least partially with adobe walls and Arabic tiles, thus potentially providing semi-natural nest-sites), new buildings are made with long lasting materials, such as bricks and concrete, that do not provide suitable cavities for nesting.

Since 1998, with the help of funding from European Union (EU) LIFE-nature conservation programmes, artificial nests have been provided to reverse declining population trends of both species (Catry et al. 2009, 2011b). New artificial nests include cavities in plastered walls (new cavities dug in existing traditional buildings that are then plastered), clay-pots and wooden nest-boxes in both traditional and new buildings, and newly built breeding walls and towers with up to 87 cavities each (Catry et al., 2009). In 2017, there were 944 artificial nest-sites available including 149 cavities in plastered walls, 663 in newly built breeding walls and towers, 65 clay-pots and 89 wooden nest-boxes. Lesser Kestrels and Rollers use all types of nests provided, can be often found in the same structures and can use the same nest-sites in alternate years (Catry et al., 2015).

2.2 Species surveys, population trends and occupation rate of artificial nest-sites

During the 2017 breeding season, the overall area to be prospected within the SPA included open/agricultural areas selected using the Corine Land Cover 2000 map. All human made buildings (including traditional and new buildings: houses, farm sheds, churches, mills, ruins, etc) were selected from military maps at 1:25,000 scale. Buildings not reported in the military maps (e.g. recent ones) but detected during fieldwork were also visited. Besides visiting buildings, all artificial nest-sites provided (including wooden nest-boxes attached to electric/telephone poles or trees) were checked for the presence of both species. Every structure was visited twice to increase the likelihood of species detection: the first visit took place between 24 April and 15 May and the second one between 16 May and 15 June. Whenever the presence of Lesser Kestrels and/or Rollers was confirmed in a structure, the number, location and type of nests (semi-natural or artificial) was recorded. The second visit was made during the chick rearing period to confirm the number of breeding pairs (and control for late breeders or failed nesting attempts, for example), resulting in minimum and maximum estimates of breeding pairs per site. The estimated population size obtained in this survey, along with the proportion of pairs breeding in semi-natural and artificial nests, was then compared with past population censuses (Lesser Kestrel: 2003 to 2007, Catry et al. 2009; Rollers: 2004 and 2009, Catry et al. 2011b).

2.3 Temporal changes in nest-site availability

In traditional buildings holding Lesser Kestrel and Roller pairs, nest shortage is an increasing threat due to building collapse (structures are only maintained through frequent conservation interventions to secure walls and roof sections). Whilst longevity of traditional buildings is unknown, Catry et al. (2009) reported that 30% of roofs from buildings monitored for Lesser Kestrels collapsed within a 5-year period and 35% of buildings holding colonies were at high risk of collapse.

To understand how the suitability (for cavity nesters) of traditional buildings changes with time, we modelled the relationship between colony size (number of breeding pairs) and time (years) using a dataset from 14 buildings occupied by Lesser Kestrels and monitored for a period of 18 years (authors, unpublished data). Each building was classified according to its degradation level, and in some years, major walls or roofs collapse and colonies disappeared. Once a building is abandoned, we predict colony size will increase initially, as new nest-sites appear with the gradual degradation of the structure, but once a certain decay threshold is reached, the number of cavities declines and the structure begins to lose its nest-sites. We used a smoothing-splines mixed-effects model ('sme' package in R, Berk 2018) to assess changes in colony size along the building degradation process. This model uses smoothing-splines to adjust the relationship between colony size (in proportion to the maximum colony capacity) and time (years), using colony ID as a random factor (Berk, 2018). The optimal model (with the correct level of smoothing) was selected according to the AIC.

Moreover, the number of future suitable traditional buildings for Lesser Kestrels and Rollers was estimated using a dataset of 175 randomly selected traditional buildings (corresponding to 56% of all traditional buildings in the area) for which suitability (presence or absence of available nest-sites) was assessed in 2008 and 2017. Buildings were considered suitable if they had at least one nest-site available (this was the only significant variable determining if a building can be used by kestrels and Rollers; see Appendix 1 for results of the logistic regression). Non-suitable buildings lack nest-sites and are generally inhabited by humans or in good conditions but may become suitable for nesting following decay. We quantified the number of buildings that became suitable (gained nest-sites following decay) and unsuitable (lost all nest-sites following structure restoration or collapse) from 2008 to 2017 and, assuming the rate of change between these years to be constant, determined the number of suitable buildings until the end of this century (using simple cross-multiplications).

2.4 Financial costs of artificial nest-sites and the potential contribution of local tourism revenues

To estimate the funding required for the conservation of Lesser Kestrels and Rollers in the area, we calculated the costs associated with the provision of artificial nest-sites needed to sustain the current population size of both species (600 and 60 breeding pairs of Lesser Kestrels and Rollers, respectively), assuming the progressive disappearance of all semi-natural nest-sites (through the collapse of traditional buildings). We estimated the number and cost of nest-sites needed in each decade until the end of the century, maintaining the current proportions of each nest type (costs of each type of nest are presented in the Appendix 2). Calculations were made for all three types of artificial nest-sites found in the area – breeding walls, clay pots and wooden nest-boxes – considering the carrying capacity (number of pairs each structure can hold), estimated longevity, production costs and occupation rate (based on data from 2017). The longevity of wooden nest-boxes and clay pots was estimated based on their average observed longevity in the last 20 years, and concrete breeding walls were assumed to last up to 50 years. We only considered costs directly associated with the provisioning of nest-sites (material, labour, transportation). Maintenance of provided nests (cleaning nest-sites before and/or after each breeding season, adding substrate to the nest, or occasionally fixing or replacing lids) were not included in the estimated costs because they are marginal when compared to the overall costs (less than 5% of the yearly provisioning costs).

We explored if tourism revenues could contribute to fund the long-term persistence of Lesser Kestrels and Rollers in the Castro Verde SPA. Local, regional and national tourism growth rates were quantified for the period between 2001 – the year before the beginning of conservation projects in the area – and 2017. We used accommodation-related metrics as our measure of tourism. Number of guests, number of nights, and lodging income (total amount paid by guests for accommodation) were retrieved from the Portuguese National Institute of Statistics (INE, 2002, 2008). Albeit not a direct measure, accommodation related metrics are easy to interpret and thus a good indicator of tourism (Rodríguez-Rodríguez & López, 2019). We then compared the Castro Verde Lodging income with the total annual funding required to sustain the current populations of Lesser Kestrels and Rollers.

3. Results

3.1 Species surveys, population trends and occupation of artificial nest-sites

A total of 412 structures were surveyed in 2017 in the Castro Verde SPA, including 388 buildings, 11 breeding walls and 13 isolated wooden nest-boxes placed on electric poles or trees. Of all structures, 151 (37%) were suitable (with at least one suitable cavity) and 67 (16%) structures were occupied by Lesser Kestrels or Rollers (54 by Lesser Kestrels, 43 by Rollers).

Lesser Kestrel and Roller population sizes were estimated at 577-625 and 58-60 breeding pairs, respectively. Both species showed increasing population trends in the study area since 2004: Lesser Kestrels increased 177% and Rollers 166% (Fig. 1). Lesser Kestrel colony size ranged from 1 to 80 breeding-pairs and the number of Rollers nesting in the same structure varied from 1 to 3 pairs. The proportion of pairs occupying artificial nest-sites also increased substantially: in 2017, 68% of all Lesser Kestrels and 66% of all Rollers were nesting in artificial nests (Fig. 1). The most used artificial nest-sites were breeding walls and towers (Lesser Kestrels and Rollers) and wooden nest-boxes (Rollers) (Table A3).

3.2 Temporal changes in nest-site availability

Long-term data of Lesser Kestrels breeding in traditional, adobe-made, buildings suggest that these are ephemeral, hosting a Lesser Kestrel colony for an average of 30 years (Fig. 2). Initially, colonies grow as the structure progressively decays and offers more cavities, with the maximum number of pairs ca. 15 years after colonization. After that, the structure decays rapidly and the number of breeding pairs is reduced by 50% just five years after peaking (Fig. 2).

From the 175 traditional buildings classified as suitable for Lesser Kestrels in 2008 and visited during 2017, 14 became unsuitable due to building collapse, 73 remained suitable, and 88 remained unsuitable but may still become suitable in the future due to ongoing or future degradation. The number of suitable buildings is expected to decrease in the future, either due to building collapse or restoration that prevents the establishment of new cavities. Based on the differences recorded between 2008 and 2017, we estimate that the number of new suitable buildings will not be able to offset those collapsing in the next couple of decades, and all traditional buildings, and hence all semi-natural nest-sites, are likely to disappear by the end of this century (Fig. 3).

3.3 Financial costs of artificial nest-sites and the potential contribution of local tourism revenues

Sustaining the current breeding populations of Lesser Kestrels and Rollers in artificial nests will cost approximately 4500€/year. This corresponds to 3260 artificial nest-sites that would need to be provided until the end of this century (ca. 360 000€, not accounting for inflation, Fig. 4), including the replacement of existing artificial nest-sites, the provisioning of new ones, and keeping the current ratio of each artificial nest-site type (please refer to figure A1 in the Appendix 2 for additional estimates considering only one type of artificial nest-site). There were differences in the cost per breeding pair between type of artificial nest provided (Kruskal-Wallis H(2)=8.33, p-value= 0.016), with breeding walls being more expensive than clay pots (difference in 2.40€, post hoc Tuckey test: p= 0.023) (Table 1).

Between 2001 and 2017, the number of tourist guests grew twice as fast in Castro Verde than in the South Alentejo region and 3 times higher the average of the full country, with an increase in 572.9% in lodging income (Table 2). In 2017, the income from lodging alone was 794 000€ in the Castro Verde area. The funds required to sustain Lesser Kestrels and Rollers in the area thus represent 0.6% of the income generated by this sub-sector of tourism.

4. Discussion

4.1 Artificial nest-sites as a reactive conservation tool

In this study we have shown that a reactive conservation approach – artificial nest-site provisioning – enabled a fast recovery and increase of Lesser Kestrel and Roller populations but made them increasingly conservation-reliant – currently more than 65% of all breeding pairs nest in artificially provided nests. Reactive conservation approaches like this may create long-term conservation traps that have been overlooked by researchers and conservationists but have major implications for the conservation of threatened populations (Cardador et al., 2015; Scott et al., 2010). There is evidence that populations of Lesser Kestrels and Rollers across their breeding ranges could be limited by the number of available nest-sites and providing artificial nests has proven to be an effective conservation tool, responsible for observed recoveries in many European countries (Iñigo & Barov, 2010; Kovacs et al., 2008) and contributing to the down-listing of the species conservation status to Least Concern (BirdLife International, 2019). We must emphasize that the availability of high-quality foraging habitats in the vicinity of the nests is also critical for maintaining positive population trends (Catry et al., 2013; Finch et al., 2018). Indeed, deterioration of foraging habitat has already been pointed out as the major driver of Lesser Kestrel's population declines outside our study area, even with the provision of artificial nest-sites (Catry et al., 2013). Whilst the extent to which both species are dependent on artificial nests across their range is unknown, other populations around Europe may face similar challenges (Kovacs et al., 2008; Rodríguez et al., 2011; Finch et al., 2018) and to maintain the population numbers of both species, artificial nests will need to be constantly provided and maintained. Our results show that the costs of maintaining healthy populations of Lesser Kestrels and Rollers could be compensated by the economic benefit provided by tourism.

4.2 Ephemerality of natural nest-sites and artificial nest-sites as conservation traps

Previous studies have already suggested that traditional buildings in the area represent temporary nest resources for birds, either due to their collapse or restoration (Catry et al., 2009; Franco et al., 2005). This study quantifies the longevity of traditional buildings and predicts the decline in number of semi-natural nest-sites over time. Traditional adobe buildings are only able to host Lesser Kestrels' colonies for roughly 30 years before collapsing Indeed, in the last 2-3 years, three out of the 14 Lesser Kestrel colonies included in Figure 2 disappeared, and two were only sustained due the provision of artificial nests (authors' personal observation).

At the current rate of movement of people from rural to urban areas, and assuming every structure currently without cavities (mostly inhabited or in good condition) would become suitable in the future, all traditional buildings and, consequently, all semi-natural nest-sites, are expected to disappear before the end of this century. Whilst we should acknowledge some limitations to our projections due to the assumption of constant rate of degradation across time (based on the rate of change observed between 2008 and 2017), the non-reversible loss of suitable traditional buildings, and hence of all semi-natural nest-sites in the short/medium-term seems unequivocal. In fact, suitable adobe-made buildings may cease to exist even sooner, as some may be restored or collapse before the appearance of nest-sites. Adobe is no longer used as a building material in the study region, which precludes the appearance of new adobe-made buildings, potentially suitable to host new colonies in the future. Therefore, the long-term persistence of Lesser Kestrels and Rollers in Castro Verde will soon be fully reliant on artificial nest-sites. The disappearance of semi-natural nests and the logistic effort to ensure the provisioning of artificial nests and guarantee the viability of the targeted species creates a conservation trap (Cardador et al., 2015).

The estimated cost to accommodate all Roller and Lesser Kestrel breeding pairs in artificial nests within the Castro Verde SPA is 4500€/year, considering the occupation rates of breeding walls and towers, wooden nest-boxes and clay pots. Although other solutions (e.g. providing only wooden nest-boxes or clay pots) could be slightly cheaper (Table 1 and Figure A1), previous studies carried out in the area showed that these nests can reach very high temperatures during hot days, leading to chick physiological stress and mortality (Catry et al., 2011a; 2015).

Whilst the recovery of both populations through nest-site provisioning was funded by government budgets, their future conservation may be jeopardized by the unsustainable need to perpetuate the implementation of conservation actions as well as by the lack of funds available to continue protecting both species. The recent down listing of Lesser Kestrels and Rollers to "Least Concern" may have thus been a hasty decision because both species still require continued conservation management and funding, even if their populations are no longer threatened according to IUCN criteria.

4.3 Funding conservation-reliant species: the potential of tourism revenues for conservation

Government budgets remains the central funding source for conservation, especially in protected areas (Emerton et al., 2006; Mansourian & Dudley, 2008; Steven et al., 2013). Major conservation budgets concentrate on funding nature-friendly management practices (e.g. through Agri-Environmental Schemes or Paying for Ecosystem Services Schemes; Batáry et al., 2015; Chakrabarti et al., 2019), or on species-specific recovery action plans that are based on a short-term response to an identified emergency threat, and usually fail to evaluate long-term threats that may persist once funding ends (Scott et al., 2010). In the Castro Verde SPA, the provisioning of new structures for cavity nesting birds is a specific measure funded through Agri-Environmental Schemes (AESs), part of the Rural Development Programme (RDP). However, this voluntary measure had no engagement by farmers and no new nest-sites were provided under this scheme (authors' personal observation).

Nature-based tourism has been increasingly seen as an opportunity to supplement government budget allocations (Steven et al., 2013), having the potential to generate enough local income to reduce the need for long-term external financing for conservation (albeit not entirely, Kiss, 2004). Birdwatching is a significant and expanding subsector of the tourism industry, where people travel to see particular bird species or areas with high endemism or diversity (Steven et al., 2013). Although it is hard to quantify the exact contribution of nature-based tourism to total tourism revenues, the increasing attention to the high natural value of the region remains unquestionable. The number of visitors to the Environment Education Centre of the LPN at Castro Verde (a national environmental NGO) increased by 300% from 2005 to 2018, as well as the supply of birdwatching tour guides (LPN, personal communication). The recent classification of the municipality as UNESCO Biosphere Reserve, highlighting Castro Verde as one of the last refuge for many globally threatened farmland birds in western Europe (Lesser Kestrels, Rollers, Little and Great Bustards, Black-bellied Sandgrouse, Iberian Imperial Eagle), has certainly played a fundamental role in raising tourism revenues. The 4500€ required to fund the provisioning of nest-sites represents only 0.6% of the total income from lodging visitors in 2017 and highlights the great potential of using local tourism revenues to fund the conservation of threatened species in the area.

Tourism and conservation can mutually support each other, especially when recognizing the rich and varied ecosystems services provided by many species (Czajkowski et al., 2014; Kiss, 2004; Steven et al., 2013; Wei et al., 2018). For example, in Poland "stork villages" generate substantial income to local communities while supporting tourism management and improving public environmental awareness (Czajkowski et al., 2014). On a much larger scale, the conservation of Giant Pandas *Ailuropoda melanoleuca* in China generates 10 to 27 times the cost of maintaining key habitats in reserves (Wei et al., 2018). The values presented in our study demonstrate the substantial economic benefits generated by bird and nature-related tourism in the study region. The Convention on Biological Diversity (CBD) has already provided guidelines for parties and other stakeholders to manage tourism activities in an ecological, economic and socially sustainable manner (CBD, 2007).

In the most likely scenario in which the maintenance of Lesser Kestrels and Roller populations will require long-term management investments, finding ways to foster self-sustainable conservation is important to guarantee the viability of targeted populations in a foreseeable future. Human-made structures have been opportunistically used for nesting by bird species throughout the globe (Mainwaring, 2015). In the Castro Verde SPA, first known settlers of Lesser Kestrels and Rollers, and still over 30% of the current population, nested in traditional human buildings, with no records of birds breeding in their original natural nests (burrows in cliffs or trees). Considering the nature-friendly reputation of the area and the income generated by tourism, it should be possible for the council to require that all new buildings should include cavities with the right dimensions for different cavity nesting species, a measure than should be included in the council building regulations.

The conservation implications presented here are not limited to the Portuguese populations of Lesser Kestrels and Rollers or even to bird species. Similar conservation challenges are likely widespread amongst other cavity nesting species from different taxa, whose populations have been recovered through the provisioning of nests following shortage of natural nest-sites (e.g. seabirds: Bolton et al., 2004; marsupials: Beyer & Goldingay, 2006; bats: Mering & Chambers, 2014). Local conservationists and researchers need to consider the long-term consequences of reactive conservation measures and search for solutions to secure the funding required to guarantee the success of these measures, as well as the viability of target populations.

5. Conclusion

In the future, conservation reliance is likely to become even more pervasive because human activities are driving more and more species towards extinction (Scott et al., 2010). This is the case for many species, such as Lesser Kestrels and Rollers, that adapted to live in human dominated landscapes and their persistence depends on the continuation of measures that promote breeding and foraging habitats. Conserving global biodiversity is a great challenge, and the budget needed to support it is likely to grow exponentially as the ranks of conservation-reliant species increases. Here we provide evidence that nature-based tourism has the potential to generate enough income to create self-sustainable conservation. But only by including a broader spectrum of society, involving public participation and political commitment (James et al., 2001; Scott et al., 2010), can tourism revenues be translated into effective conservation measures and foster the long-term viability of wildlife populations.

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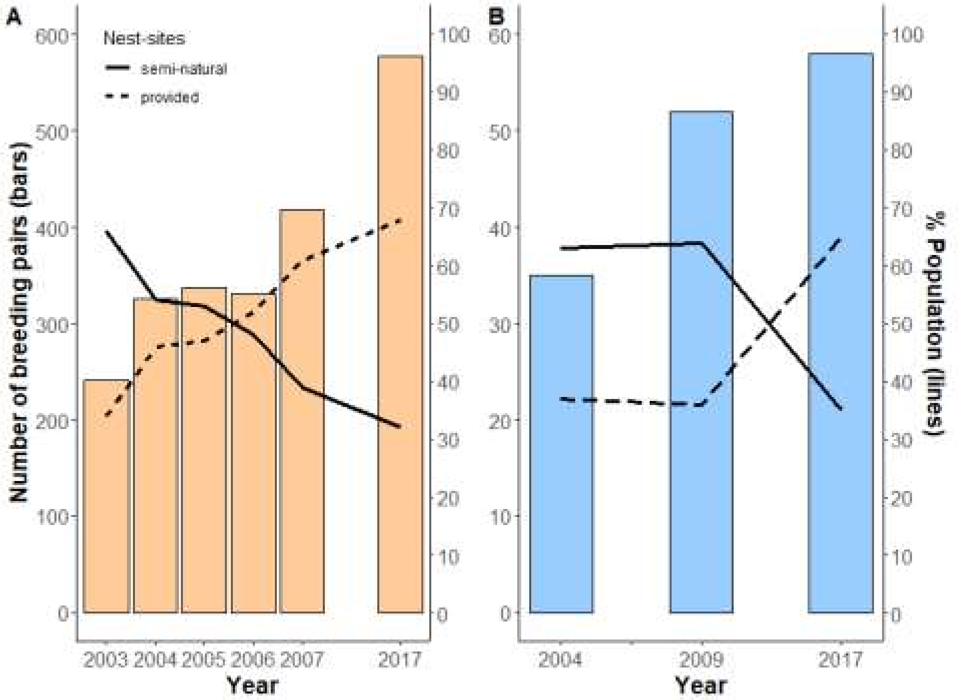

Figure 1: Population trends (bars) of (A) lesser kestrels and (B) European Rollers in the Castro Verde SPA, south Portugal (bars), and proportion of pairs occupying semi-natural (solid line) and artificial (dashed line) nest-sites. Presented values show minimum survey estimates.

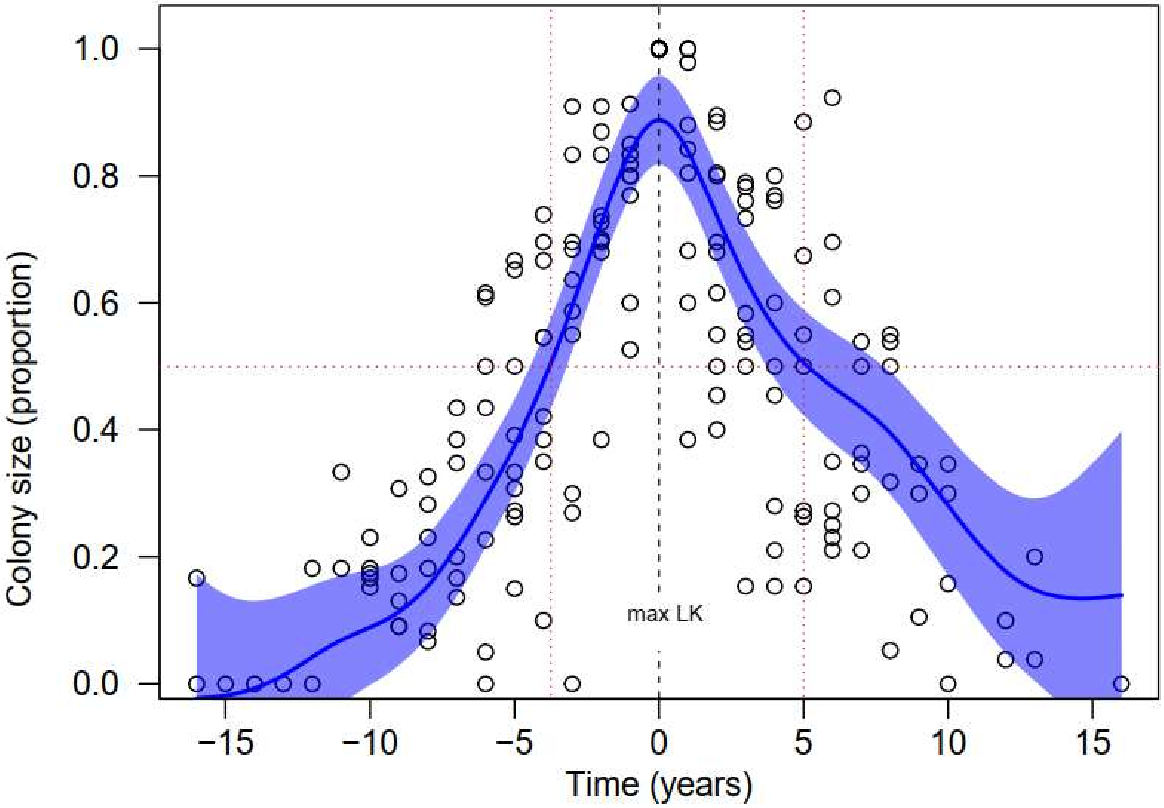

Figure 2: Temporal changes in size of lesser kestrel colonies (n=14) established on traditional adobe-made buildings. The trend line was estimated using a smoothing-spline mixed-effect model (loess) selected according to the AIC. Shaded area represents 95% confidence intervals. Dots represent colony size in relation to its maximum (year 0, max LK). The vertical lighter lines encompass the period when colonies were within the 50% of their maximum size. Results suggest the average longevity of a Lesser Kestrel colony in traditional buildings is less than 30 years.

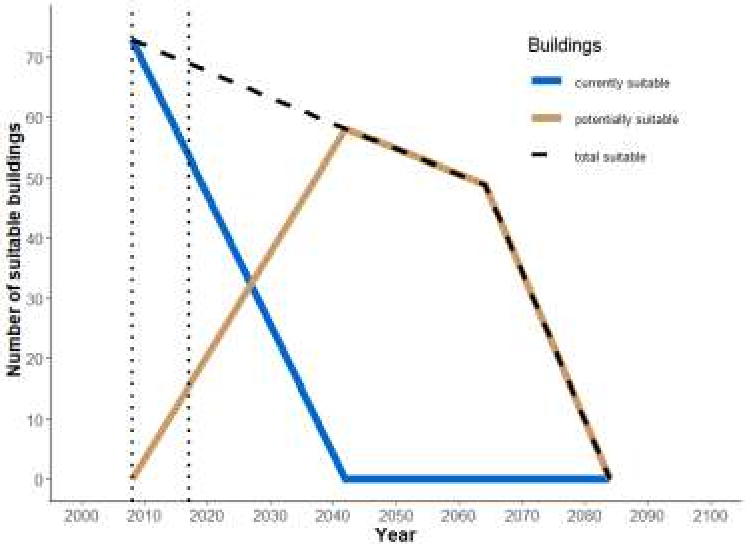

Figure 3. Projected changes in the availability of traditional adobe buildings, suitable for breeding Lesser Kestrels and Rollers, during the next hundred years. Potentially suitable (those currently unsuitable but likely to become suitable due to natural degradation after abandonment) are predicted to increase at first but the gradual collapse of all structures will lead to the disappearance of all semi-natural nest-sites before 2100. Projections are based on the observed rate of change of 175 buildings between 2008 and 2017 (between dotted vertical lines).

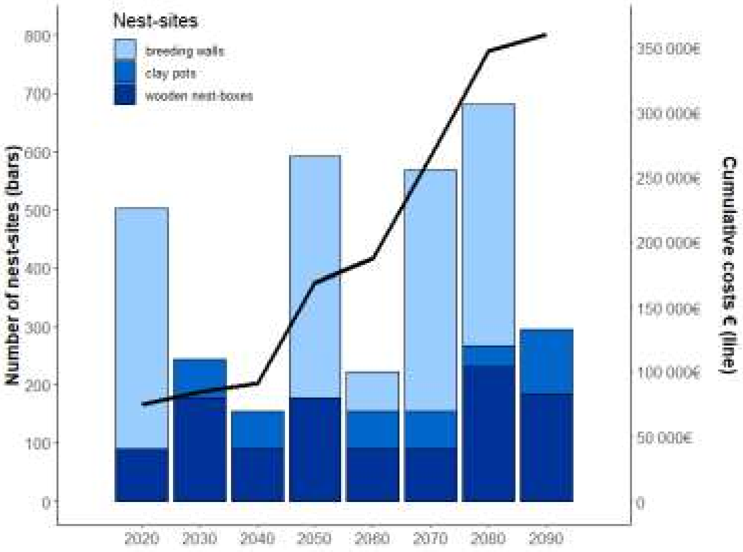

Figure 4: Conservation costs by decade (columns) and cumulative (black line) to sustain the current populations of Lesser Kestrels and European Rollers in the Castro Verde SPA, southern Portugal. Estimates by decade account for the replacement of provided artificial nest-sites at the end of its lifespan and new nests to accommodate all breeding pairs currently using semi-natural nests.

Table 1: Characteristics of artificial nest-sites provided in the Castro Verde SPA and estimated costs per breeding pair. The occupation rate was calculated based on the survey conducted in 2017.

Lesser Kestrel + Rollers	**Number of nest-sites**	**Average Occupation rate 2017**	**Longevity (years)**	**Production costs (€)**	**Average cost/pair ± CI (€)**
Breeding walls	69 (average)	0.44 ± 0.10	50	12 000	8.6 ± 1.7
Clay pots	1	0.73 ± 0.18	15	65	6.2 ± 1.7
Wooden nest-boxes	1	0.52 ± 0.19	7	30	7.3 ± 1.7
Rollers					
Isolated nest-boxes	1	0.44	7	30	10.95 (7.31 – 19.25)

Table 2: Growth rate of tourism (2001-2017) and lodging income (2017) for the Castro Verde municipality, the South Alentejo region (including Castro Verde) and mainland Portugal.

Region	Growth rate 2001-2017 (%)			Lodging income 2017 (thousand €)
	Number guests	Number nights	Lodging income	
Castro Verde	524.6	360.5	572.9	794
South Alentejo	248.8	254.8	338.9	13 201
Portugal	155.0	94.8	184.9	2 737 998

Appendix 1

In order to define what a suitable building was, we performed a binomial logistic regression for the presence/absence of each species in buildings with at least one available nest-site. We excluded isolated nest-boxes in trees or electric poles for the Lesser Kestrel model as they only very seldomly nest in these. Therefore, total sample size was 141 and 153 (out of the 412) buildings for the Lesser Kestrel and the Roller model, respectively. Explanatory variables for the Lesser Kestrel model were: human use, type of wall, type of roof, surrounding habitat, total number of available nest-sites, total number of available nest-sites, distance to nearest Lesser Kestrel colony (in meters), size of nearest Lesser Kestrel colony (number of breeding pairs), and number of species of other cavity-nesting birds. For the Roller models, we added distance to nearest structure with Rollers and number of Roller pairs in that structure, and removed type of roof, as Rollers do not nest under tiles. Variables were evaluated by model averaging using a subset based on a variation in Akaike Information Criterion by less than 2 units (ΔAIC<2) and looking at the p-values of full models and at the lower and higher confidence bounds of each variable estimate.

The total number of available nest-sites in a structure was the only variable that positively influenced the occupancy of a structure by both Lesser Kestrels and Rollers and had the highest relative importance in both models (tables A1 and A2). Suitable habitat was only positively selected by Lesser Kestrels, while isolated nest-boxes were selected by Rollers. All other variables, including different types of wall material and different degrees of human use, did not influence the probability of a structure being occupied by either species. We thus define a suitable structure as a structure with at least one available nest-site.

Table A1: Lesser Kestrel full-model averaging using a subset of ΔAIC<2. Variables are ranked according to their relative importance (proportion of the number of times they appeared in the model. Relevant variables were the ones where confidence intervals (CI) did not include 0 (zero).

Lesser Kestrel model

Variable	Estimate	CI	Relative importance
Total number of available nest-sites	**0.15**	**0.06 - 0.25**	**1.00**
Suitable habitat	**2.22**	**0.55 - 3.99**	**0.98**
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.84
Roof: Arabic tiles	-0.21	-1.68 - 1.04	0.64
Roof: no roof	-1.24	-3.90 - 0.02	
Size of nearest Lesser Kestrel colony	0.00	-0.04 - 0.03	0.26
Wall: adobe walls	-0.21	-3.35 - 0.99	0.18
Wall: stone walls	-0.16	-4.44 - 2.68	
Human use: abandoned	-0.03	-2.54 - 1.52	0.06
Human use: sporadic use	-0.01	-2.04 - 1.68	
Human use: intensive use	-0.04	-2.90 - 1.49	
Intercept	-2.26	-4.78 - 0.26	

*Table A2***:** *Roller full-model averaging using a subset of ΔAIC<2. Variables are ranked according to their relative importance (proportion of the number of times they appeared in the model. Relevant variables were the ones where confidence intervals (CI) did not include 0 (zero).*

Roller model

Variable	Estimate	CI	Relative importance
Total number of available nest sites	**0.17**	**0.05 - 0.29**	**1.00**
Suitable habitat	18.01	-3019.14 - 3055.58	0.99
Wall: adobe wall	3.27	-0.49 - 7.29	0.96
Wall: isolated nest-boxes	**5.31**	**1.23 - 9.88**	
Wall: stone wall	3.77	-0.79 - 8.61	
Number of Roller pairs in nearest structure with Rollers	-0.27	-1.44 - 0.28	0.46
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.38
Size of nearest Lesser Kestrel colony	0.00	-0.02 - 0.05	0.32
Distance to nearest Roller	0.00	0.00 - 0.00	0.30
Human use: abandoned	-0.08	-3.16 - 1.24	0.08
Human use: sporadic use	-0.06	-2.90 - 1.35	
Human use: intensive use	0.00	-2.35 - 2.38	
Intercept	-22.37	-3041.70 - 2996.95	

Appendix 2

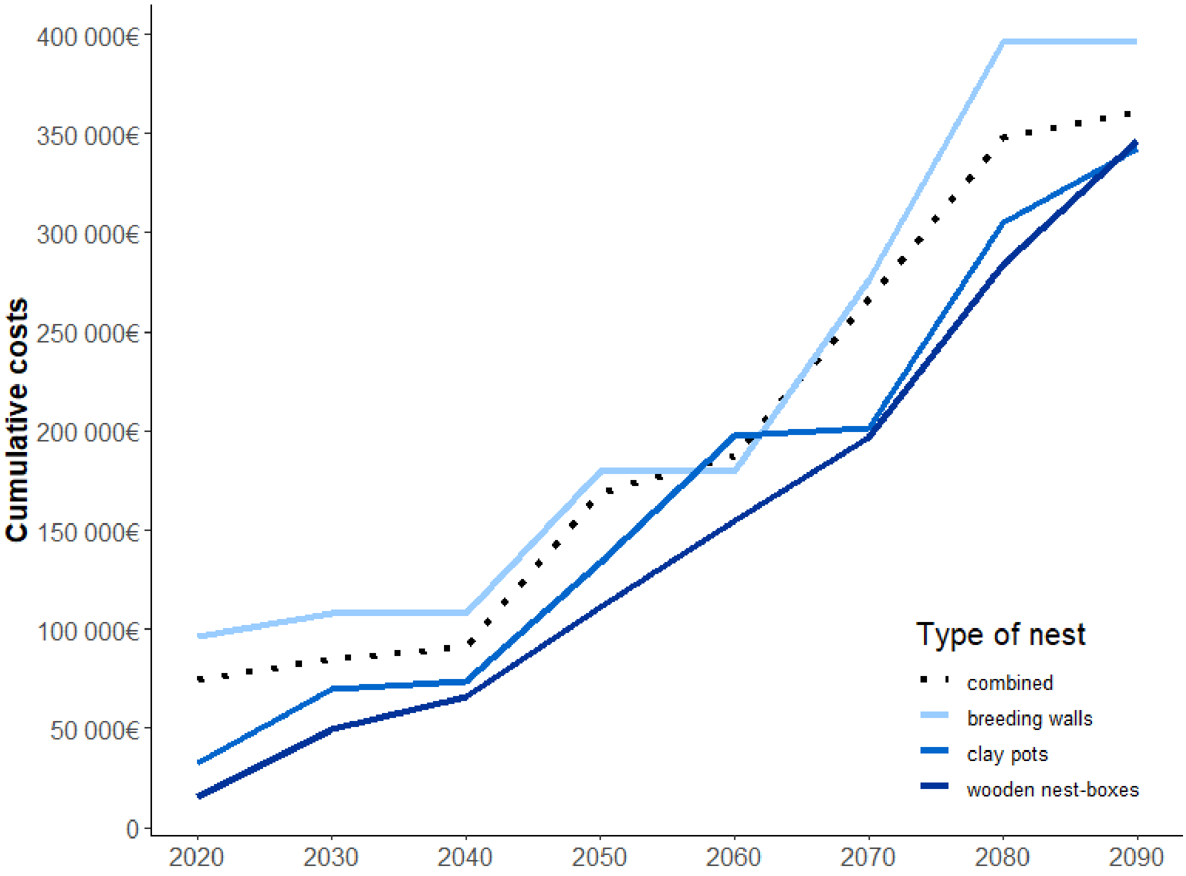

Figure A1: Cumulative conservation costs to sustain the current populations of Lesser Kestrels and European Rollers in the Castro Verde SPA, southern Portugal. Different scenarios, considering the provisioning of only one type of artificial nest-sites (solid lines) and combining the three types (dotted line, the original provided in the main manuscript) are shown for comparison. Estimates by decade account for the replacement of provided artificial nest-sites at the end of its lifespan and new nests to accommodate all breeding pairs currently using semi-natural nests.

Appendix 3

Table A3: Percentage of the Lesser Kestrel and Roller populations of the Castro Verde SPA in each type of nest (2017).

Type of nest		Lesser Kestrels (%)	European Rollers (%)
Semi-natural	Under tiles	12	0
	Semi-natural cavities	20	33
Artificial	Plastered walls	19	12
	Breeding walls/towers	36	22
	Clay pots	7	10
	Wooden nest-boxes	6	22