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The price of success: integrative long-term study reveals ecotourism impacts on a flagship species at a UNESCO site

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Abstract

Disturbance of wildlife by ecotourism has become a major concern in the last decades. In the Mediterranean, sea-based tourism and related recreational activities are increasing rapidly, especially within marine protected areas (MPAs) hosting emblematic biodiversity. We investigated the impact of ecotourism in the Scandola MPA (UNESCO World Heritage Site, Corsica island), on the population of a conservation flagship, the Osprey *Pandion haliaetus*. Over the 37-year study period, tourists flow increased sharply. Osprey breeding performance initially increased, but then dropped for pairs nesting within the MPA compared to those breeding elsewhere in Corsica. We examined several hypotheses that could explain such reduction in breeding performance. Recent osprey breeding failures in the MPA are not caused by food scarcity. Using underwater fish surveys, we showed that fish consumed by ospreys were more numerous within the MPA. Focal observation at nests revealed that the overall number of boat passages within 250 m of osprey nests were three times higher inside the MPA compared to a control area. Elevated boat traffic significantly modified osprey time-budgets, by decreasing prey provisioning rate by males, and increasing time spent alarming and flying off the nest in females. This caused stress, and corticosterone levels in chick feathers were three times higher in high-traffic areas compared to places with lower touristic flow in Corsica, the Balearic Islands and Italy. Overall, our integrative, long-term study demonstrates the negative impact of sea-based ecotourism on the Corsican osprey population. This stresses the worldwide importance of rigorously implementing sustainable ecotourism, within well-enforced MPAs.

Introduction

There is a wide consensus upon the importance of protected areas for preserving biodiversity (Fraser & Bernatchez, 2001; Le Saout *et al.*, 2014). With over 120 000 protected areas (PA) worldwide and *c.* 13% of global terrestrial habitats covered, protected area networks represent the prime conservation tool for global biodiversity maintenance (Steven, Castley & Buckley, 2013). This designation of conservation units is often motivated by the protection of flagship species, which is an efficient way to gain support from the public and to attract funding. Such charisma is often ecologically justified

(Sergio *et al.*, 2006; Cabeza, Arponen & Van Teeffelen, 2008), whereby large predators serve as umbrella species allowing the conservation of entire communities (Crooks & Sanjayan, 2006; but see also Hausmann *et al.*, 2017).

Due to limited governmental funding for conservation, ecotourism is now contributing substantially to the funding of PAs. This financial, but also political support conveys evident benefits for the conservation of threatened species (Steven *et al.*, 2013). In this sense, ecotourism provides net conservation gains and is increasingly advocated as a tool in global conservation (Buckley, Morrison & Castley, 2016). Yet, ecotourism can have direct ecological impacts, with a

range of negative environmental effects on fauna (Steven, Pickering & Castley, 2011). Ecotourists engaged in nature-based tourism and recreation (such as hiking, cycling, running) may become a threat for local biodiversity, including the wildlife they are keen to observe in its natural habitat (Buckley, 2004; Pauli, Spaul & Heath, 2017). This is the case for grizzly bears *Ursus arctos* in North America (e.g. Hood & Parker, 2001), Amur tigers *Panthera tigris altaica* in Russia (Kerley *et al.*, 2002) or Imperial Eagles *Aquila aldalberti* in Spain (González *et al.*, 2006). Overall, there is an extensive set of studies examining impacts of nature-based recreation on wildlife (reviewed in Buckley, 2004; Martinez-Abrain *et al.*, 2010; Steven *et al.*, 2011), with the majority of them occurring inside PA, both terrestrial and marine (MPA).

Similar to terrestrial reserves, marine protected areas (MPA) are an essential conservation tool in the marine environment (Leenhardt *et al.*, 2013; Lubchenco & Grorud-Colvert, 2015); MPAs proved to be efficient tools for the preservation of benthic communities (Selig & Bruno, 2010), of the pelagic realm and its associated top predators (Pichegru *et al.*, 2010; Aburto-Oropeza *et al.*, 2011; Péron *et al.*, 2013). However, MPAs are being marketed for ecotourism, and therefore tend to attract more visitors than 'unprotected' areas. This leads to a potential direct disturbance by recreational activities, which have been already reported for fish (e.g. Bracciali *et al.*, 2012), seabirds (McClung *et al.*, 2004; Velando & Munilla, 2011) and related marine habitats (e.g. Lloret *et al.*, 2008). Much of this research has been focused on the immediate effects of ecotourism (e.g. direct disturbance, changes of behavioural activities, breeding failures). In contrast, there is still limited information on long-term consequences on population dynamics, preventing adequate management.

Herein, we present an integrative study of the impact of tourism-associated activities on the Scandola MPA and its emblematic raptor, the Osprey *Pandion haliaetus*. The osprey is a flagship species for conservation across its vast distributional range (Monti *et al.*, 2015). It is often seen as a symbol of nature comeback, saved from extinction after periods of intoxication by pesticides and direct persecutions, by successful direct management actions and reintroduction programmes (Poole, 1989). In North America and Europe, several regional socio-economic marketing strategies (e.g. ecotourism) are tightly linked to the presence of ospreys (e.g. Loch Garden and Rutland Water in the UK). They also serve as 'boundary objects' (*sensu*: Star & Griesemer, 1989) enhancing the awareness of the public, and of policy makers, with respect to environmental issues. This is very much the case in the Mediterranean region, where the presence of ospreys facilitates the establishment and adequate management of reserves in Morocco (Al Hoceima National Park), Italy (Maremma Regional Park), Spain (embalse Guadalcacin, Barbate reservoir in Andalucia) and France (Scandola reserve, Corsica) (Monti, 2012; Monti *et al.*, 2013, 2014).

In the Mediterranean, the osprey is associated with the marine environment, where it feeds exclusively on live, epi-pelagic fish. Ospreys mainly nest on sea-cliffs, at heights between 5 and 30 m (Poole, 1989). The island of Corsica currently hosts the largest osprey population in the Mediterranean, with a breeding nucleus of *c.* 30 pairs (37.5% of the entire estimated Mediterranean population; Monti, 2012).

In this study, we aimed at understanding to what extent the development of ecotourism and the management of the MPA of Scandola affected the Corsican osprey population, and tested two hypotheses which are mutually non-exclusive: (1) the MPA, since its creation, had a positive incidence on osprey population dynamics. In particular, we postulated that the establishment of the reserve might have played an important role in producing multiple indirect benefits such as (a) better protection of birds because of reduced human disturbance; and (b) greater food availability in terms of fish abundance, fostered by the reduced fishing quota inside the MPA (Francour *et al.*, 2001). As a second hypothesis, we postulated that (2) the Scandola MPA generated additional constraints, due to sea-based tourism and recreational activities, called for by the existence of the MPA, unique landscape features and the presence of emblematic ospreys. In this context, our specific goals were as follows: (a) to reconstruct historical trends of the sea-based tourism expansion in Corsica and to confront those with historical osprey population trends and breeding parameters; (b) to quantify the potential benefits for osprey of MPA compared to the rest of Corsican coast (abundance of prey) and drawbacks (ecotourism generated by the MPA in recent years, using boat traffic as a proxy) and (c) to assess the effect of boat traffic on osprey adult behaviour and consequences on chick stress (using corticosterone levels as a proxy following Bortolotti *et al.*, 2008).

Our integrative analyses have important general implications for protected area design and management, and for the conservation of Mediterranean biodiversity. This study is a clear example of broader wildlife-based and cultural tourism issues, representing a neglected cause of current biodiversity decline. Many species, especially those with substantial habitat requirements, are going in conflict with people for space and resources (Buckley *et al.*, 2016). Therefore, socio-economically viable decisions that guarantee the persistence of animal populations are timely and of central concern for conservation.

Materials and methods

Study area

This study was conducted along the 250 km of the west coast of Corsica (France), from Cape Corse in the North, to Ajaccio in the South, where the entire Corsican osprey population breeds (Thibault, Bretagnolle & Dominici, 2001; Fig. 1a). The study area includes the Scandola MPA (42°36′N, 8°56′E), which is a terrestrial and a marine reserve of *c.* 2000 ha, created in 1975, and declared as UNESCO World Heritage Site since 1983 (Fig. 1b). Scandola is almost exclusively visited by sea, with *c.* 300 000 visitors concentrated between June and August, aiming to observe scenic geologic formations and osprey nests (Richez & Richez Battesti, 2007; Tavernier, 2010). Regulations of MPA restrict the access to 12 local professional fishermen but no limit is
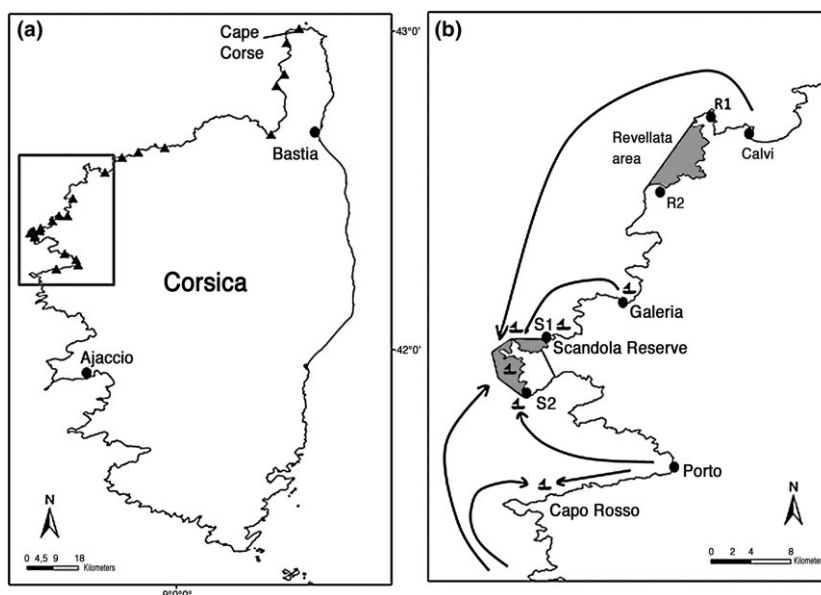
Figure 1 (a) Location of osprey nests in Corsica, where the 24 transects of fish sampling have been performed (see Appendix S1: Fig. 1c–d); (b) zoom on the Scandola marine protected area and the Revellata areas (coloured in grey); for each area land-based vantage-points are reported as: S1, S2, R1, R2; harbours (black dots), main touristic boat circuits (arrows) and high-traffic areas (ship symbol) are also included, according to: Richez & Richez Battesti, 2007; Tavernier, 2010).

set upon the number of visiting vessels and the distance of approach to the coastline (e.g. usage, zonation and fishing efforts in the MPA are described in detail in Francour *et al.*, 2001; Le Diréach *et al.*, 2010).

Prey resource availability

We assessed prey availability to ospreys at 24 sites hosting osprey nests along the west coast of Corsica (eight sites inside and 16 sites outside the MPA; Fig. 1a), using video recording surveys. Surveys were performed twice each year at each site, and the monitoring protocol was repeated in 2012 and 2013, yielding a total of 96 sampling sessions. Details of corresponding methods and results are presented in Appendix S1.

Historical osprey population dynamics

The Corsican osprey population has been monitored since 1977 (Thibault *et al.*, 2001; Bretagnolle, Mougeot & Thibault, 2008). Available historical breeding data used for our analyses covered a 37-year period (1977–2014). For each nest site and each year, the following parameters were recorded: number of eggs laid, number of eggs hatched and number of chicks fledged. From these, we calculated an annual breeding success (young fledged/eggs laid), hatching success (young hatched/eggs laid) and fledging success (young fledged/eggs hatched). Nests were grouped with respect to their position outside/inside of the MPA. We fitted generalized linear mixed-effect models (GLMMs) using the above-cited breeding parameters as response variables. We tested for the effect of the MPA by including a binary

variable (0 = 'out of the MPA' or 1 = 'inside MPA') as a fixed factor. We accounted for potential temporal effects in two ways. First, we considered a linear trend with 'time', using the number of years elapsed since the MPA's creation in 1975 as a predictor. Second, since Bretagnolle *et al.* (2008) found density-dependent effects upon breeding parameters occurring after 1990, we also analysed processes using this year as threshold for change. 'Nest' was included as a random effect, to avoid pseudoreplication at the level of territories. A Poisson error distribution was set *a priori*, for discrete random variables (count data; cf. Zuur *et al.*, 2009; Bolker *et al.*, 2009). The binomial error distribution was used for proportion data (Crawley, 2007), that is, hatching, fledging and breeding success. Akaike's Information Criterion corrected for small sample sizes (AICc) was used as a tool for model selection. Models were retained for inference if ΔAICc $\leq$ 2 units, and if their AICc value was lower than that of any simpler, nested alternative (Richards, 2008; Richards, Whittingham & Stephens, 2011). We selected among all models using the 'dredge' function in the R package 'MuMIn' (Bartoń, 2012), fitting all biologically meaningful possible models. Model coefficients were estimated for selected models, using the 'confint' function. All statistical analyses were conducted in R 2.15.0 (R Core Development Team, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org). Data summaries are reported as mean $\pm$ SD.

Behavioural observations

Between 2012 and 2014, focal observations at osprey nests were carried out from vantage-points located at a distance of

more than 300 m from occupied nests. Each nest was monitored at least once from 6:00 to 20:00 and, when possible, we repeated observations for 2 or 3 days. Focal animals were observed with binoculars and a 60× telescope to record specific behavioural patterns, such as time spent at nest by the pair as a proxy for parental care (e.g. McClung *et al.*, 2004), successful fishing, chick feeding alarm calls and flights triggered by boat passages. In particular, following standard criteria for osprey behaviour classification (Bretagnolle & Thibault, 1993), we considered the following variables: (a) number of prey items brought to the nest per hour; (b) number of disturbing events (e.g. an approaching boat to the nest); (c) number of occasions at which parents left the nest after a disturbing event (number of flight off events) and (d) total amount of time spent by the female alarming for an approaching boat. For all nests, we compared these four behavioural variables across different sampling days (3 days). For this comparison, all nests were observed in different days, which involved repeated observations for each nest. Behavioural data were not normally distributed, so we compared them across days through the Friedman test, a non-parametric test suitable for k-related samples (Friedman, 1937). Then, for each behavioural variable, we also tested whether birds from a nest located along tourist shuttle circuit behaved differently than birds nesting in low-traffic sites (Fig. 1b); a binary variable 0 = 'low traffic' or 1 = 'high traffic' was used as fixed factor in GLMMs, using the above-cited behavioural parameters as response variables. 'Nest' was included as a random effect and model selection was conducted as stated in section Historical osprey population dynamics. Note that the tourist shuttle circuits included all Scandola MPA and also a few adjacent shorelines where a few osprey nests were present as well, so all these potentially disturbed sites were included in the 'high-traffic' area (Fig. 1b). Since osprey time-budgets as observed at the nest are also strongly shaped by human disturbance, we used a classification based on the intensity of tourist boat traffic. Thereby, six nests were located in 'high-traffic' areas (the three nests inside MPA and three other nests outside MPA but close to it and frequently visited as well), and 7 in 'low-traffic' areas (all outside MPA).

Home ranges and feeding areas of breeding ospreys

To estimate feeding areas and home ranges of breeding ospreys, nine adult individuals (two males and seven females) were trapped and equipped with GPS transmitters. Trapping methods, devices' features and details of corresponding spatial analyses are reported in Appendix S2.

Tourism and boat traffic evaluation

We assessed the at-sea boats' distribution and frequency of passages by means of specific monitoring protocols, conducted both in 2013 and 2014. Number of entrances and exits of boats from the MPA and from a control area were recorded. Boat passages were considered in relation to specific distance categories to focus on boats which were more likely to disturb ospreys. Details of corresponding methods and results are described in Appendix S3.

Stress level of chicks

We sampled body feathers of osprey chicks to measure corticosterone levels, to estimate their stress levels during the chick-rearing period (Bortolotti *et al.*, 2009; see Appendix S4). Feathers were collected during one single event of disturbance, during ringing activity at nests. Such single acute stress does not leave its signs in growing feathers (Bortolotti *et al.*, 2008). Rather, corticosterone levels measured in feathers are an indication of chronical stress (Bortolotti *et al.*, 2008), as that generated by repeated disturbance by vessels. Corticosterone levels can be evaluated, integrating time periods from a few days to many weeks within a single feather. The hormonal response can be linked directly to behavioural interactions (i.e. aggression) and/or acute environmental perturbations (e.g. inclement weather) (Bortolotti *et al.*, 2008). Since corticosterone deposition in growing feathers proceeds with the growth rate and is a relatively slow process (e.g. it can take several days or weeks; Bortolotti *et al.*, 2009), we are confident that corticosterone content in the sampled feathers was not altered by the single, short event of disturbance at the time of sampling. Following the previous classification for boat traffic, we distinguished samples collected at nests in high- ($n = 4$) and low- ($n = 5$) traffic areas. As a control, we also included samples from chicks from Italy ($n = 4$) and the Balearic Islands ($n = 5$) from undisturbed areas. Initially, we compared corticosterone levels of feathers between nests in high-traffic areas and those in low-traffic areas, through a Mann–Whitney U-test. Then, we compared hormonal levels across high-traffic, low-traffic, Italian and Balearic sites through a Kruskal–Wallis test.

Results

Historical trends in population and breeding parameters

We analysed a total of 745 nest-data occurrences across a 37-year period (from 1977 to 2014). The osprey population increased from 3 to a maximum of 34 breeding pairs (in 2011). Numbers of pairs and chicks fledged as well as reproductive parameters (hatching, fledging and breeding success) varied substantially over time (Fig. 2).

We found no significant differences in the average number of eggs laid per nest for pairs breeding inside or outside the MPA (Appendix S5a, b; Fig. 3a). Our models give some support for an interaction effect between 'Outside/Inside MPA' and 'time' on the number of eggs hatched, with a decrease within the MPA, but not outside (Appendix S5a, b; Fig. 3b); but note that the null model has similar support. The number of chicks fledged was also influenced by the
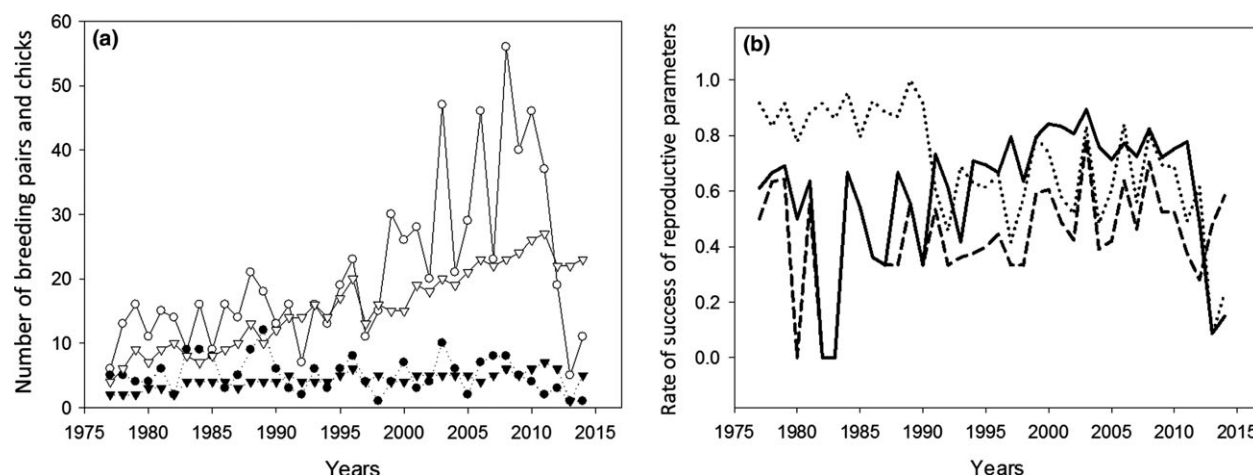
Figure 2 Historical trend of the Corsican osprey population in 1977–2014: (a) number of breeding pairs and chicks fledged outside of the marine-protected area (MPA) (white triangles and dots, respectively) and inside the MPA (black triangles and dots, respectively); (b) hatching success (dashed line), fledging success (dotted line) and breeding success (solid line) in the whole Corsica, over time. These trends are obtained directly from the data (i.e. not modelling involved).

interaction between 'time' and 'Outside/Inside MPA': there was no evidence of a significant change of this index over years for territories outside the MPA, while there was indication of a reduction inside the MPA (Appendix S5a, b; Fig. 3c). Analyses are suggestive of an effect of 'time' and 'Outside/Inside MPA' also for hatching success (Appendix S5a, b; Fig. 3d); we note however limitations in model fit in this analysis. While the model suggests an increase for hatching success 'Outside MPA', raw data points suggest a decrease (Fig. 3d). Fledging success showed a general decrease over time in Corsica as a whole (both inside and outside MPA), but the interaction between 'time' and 'Outside/Inside MPA' was not supported by model selection (Appendix S5a, b; Fig. 3e). Breeding success decreased strongly over years for pairs breeding inside the MPA compared to those nesting outside (Appendix S5a, b; Fig. 3f). When testing for a density-dependent effect (using 1990 as a threshold year), all breeding parameters significantly declined after 1990 in the MPA, except for the number of eggs laid which did not change between periods (Appendix S5a, b). Finally, annual trends for breeding success were correlated to the transport capacity of touristic shuttles (number of passengers) outside the MPA, but not inside (Fig. 4).

Effect of boat traffic on behaviour and stress

Overall, 41 days of observations (*c.* 570 h) were carried out over the 3 years at 13 nest sites. Most nests inside MPA failed (chicks died) during the observation period (in line with low breeding success recorded inside MPA, during last years). For this reason, only a few nests were available for observation within the boundaries of the MPA. This explains the limited sample size of observable nests for the MPA compared to nests outside of the MPA, and hence the

necessity to increase the number of observation days to collect behavioural data. For this analysis, nests were classified as stated in methods. Six nests were observed for 2 days and six for 3 days, and only 1 nest for 1 day. We found no significant differences among 2- or 3-days repetitions in any of the behavioural patterns considered for each nest (Friedman test for each behaviour: all $P > 0.05$). Data were therefore pooled across day-repetitions.

The number of prey items brought to the nest per hour was 50% lower for nests located in high-traffic areas (Appendix S5c, d; Fig. 5a). At these nests, the occurrence of disturbing events was also six times greater than at low-traffic areas (Appendix S5c, d; Fig. 5b). The number of occasions at which parents left the nest after a disturbance tended to be higher for high-traffic areas, even if the model was not significantly supported (Appendix S5c, d). Females rearing chicks at high-traffic sites spent more time alarming for an approaching boat (Appendix S5c, d).

To evaluate chick stress levels, we tested both the concentration (ng mg^{-1}) and the temporal expression of corticosterone (ng mm^{-1}) in feathers. In both cases, we found that values for chicks from high-traffic areas were significantly higher than those recorded at other nests in Corsica (Mann–Whitney U-test: $U = 1.0$; $P = 0.027$; $N = 9$) and at non-disturbed nests in general (i.e. including control samples: Mann–Whitney U-test: $U = 1.0$; $P = 0.004$; $N = 18$) (Fig. 6). Values also differed when considering each location separately (Fig. 6; Kruskal–Wallis: $\chi^2 = 11.42$, d.f. = 3, $P = 0.010$, $N = 18$).

Discussion

Our extensive, long-term and multidisciplinary dataset allowed a detailed investigation of the incidence of the current management of the Scandola MPA on the status of a Mediterranean conservation flagship species, the osprey. This
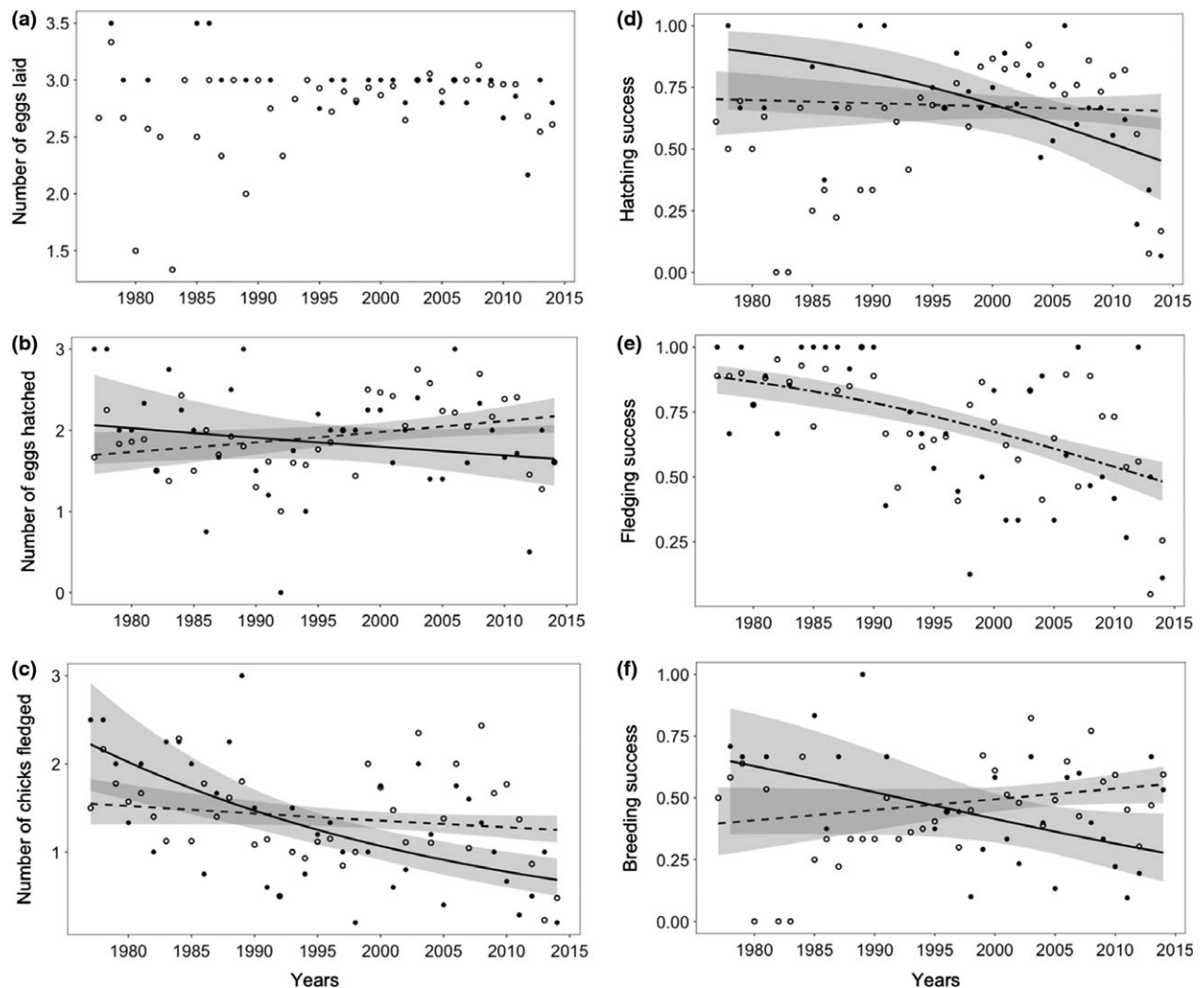
Figure 3 Historical trend in Corsican osprey breeding parameters inside the Scandola marine-protected area (MPA) (black dots and solid line) and outside MPA (white dots and dotted line): (a) number of eggs laid; (b) number of eggs hatched; (c) number of chicks fledged; (d) hatching success; (e) fledging success (dashed line for the whole Corsica) and (f) breeding success. 'time' and 'outside/inside MPA' models were used to produce predictions in these graphs. Dots represent raw data and lines estimates of the selected model from generalized linear mixed-effect model (see Appendix S5). Confidence regions (0.95 confidence intervals) of the selected models for each reproductive parameter are also represented by semi-transparent shades.

unique information allowed to validate our two working hypotheses: (1) initially, the MPA had a positive effect on the Corsican osprey population, yet (2) following recent increase in ship traffic, ospreys breeding at sites inside the Scandola MPA are now being critically disturbed, and their breeding performance has dropped despite the fact that they exploit fish resources which are more abundant than outside of MPA (Appendix S1). Our case study gives a powerful example of a negative impact on MPA linked to ecotourism, calling for much caution in the management of protected areas at the international level, and specifically for well-enforced MPAs (*sensu* Edgar *et al.*, 2014).

Mediterranean ospreys belong to a small population which has been exposed to intense, direct persecutions since 19th century, before being fully protected in 1976 (Poole, 1989).

This most certainly explains their marked sensitivity to disturbance when compared to other populations, like in North America. In our specific case, breeding ospreys seemed to be accustomed to the presence of boats at sea, at least until they approach too close (less than 250 m) to nests.

We found declines in osprey breeding parameters over time for pairs breeding inside of MPA, compared to those breeding outside of MPA. Although this may also be partly explained by density-dependent population regulation processes (Bretagnolle *et al.*, 2008), we show that the MPA played an important role in shaping population trends over time. We acknowledge that our results may be affected by our choice of model structure. This includes the fact that we only considered a linear trend with 'time', which limits the extent to which our estimated trends could fit the data. In
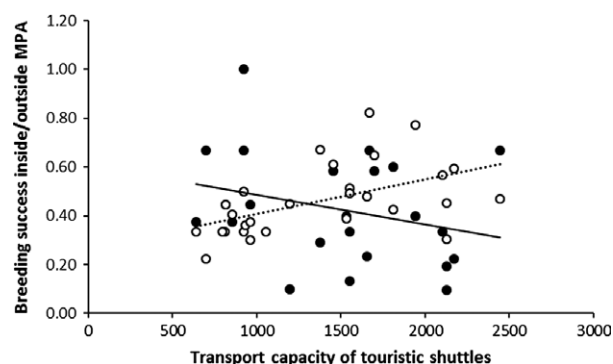
Figure 4 Correlations between breeding success inside the marine-protected area (MPA) (black dots and solid line; Spearman's rank correlation, rho = −0.289, $P = 0.181$) and outside the MPA (white dots and dotted line; rho = 0.557, $P = 0.002$) and transport capacity of touristic shuttles (calculated as stated in Appendix S3) in Corsica.

particular, this may have affected our analyses of hatching success, where our data points suggest a decrease over the last two years, while our model suggests an increase (see Fig. 3d), hence this result needs to be interpreted with care. Fit to the linear trend appears reasonably good for the remaining analyses. However, Bretagnolle *et al.* (2008) reported a temporal increase in nest density in the central, historical breeding area (from Calvi to Porto). This area encompassed nests both located inside and outside of MPA (e.g. sites in the Revellata or Capo Rosso areas, see Fig. 1b). Therefore, disturbance by boat traffic and density-dependence processes acted simultaneously across these sites. Nevertheless, our results showed contrasting trends between the two categories (inside/outside MPA): nests for which breeding parameters were negatively affected were mostly located inside the MPA.

To clarify the proximate causes of such issue, two hypotheses could be developed:

1 Local prey abundance affects osprey breeding success. As expected, sites inside MPA hosted greater fish populations with larger body size (and, consequently, higher biomass) than sites outside MPA. This is because the Scandola MPA is one of the most pristine sites for marine biodiversity in the Western Mediterranean basin, with all marine biotas and trophic webs well-preserved (Francour, 1994; Francour *et al.*, 2001). These positive effects of MPA are substantial for the local fish fauna, including species predated by ospreys (Francour & Thibault, 1996; Francour *et al.*, 2001; Guidetti *et al.*, 2014). Therefore, the MPA played a positive role, by providing abundant food resources to ospreys. These results are coherent with GPS-tracking of breeding adults (Appendix S2), which showed that their feeding home ranges were extremely small, and largely confined to coastal areas adjacent to breeding sites, both inside and outside MPA.

2 Massive boat traffic inside MPA, linked to sea-based tourism, explained the recent decline in osprey breeding performances. As Morvan (2010), we found that touristic boat traffic was much more intense inside MPA than outside (especially in July during the high tourist season). Furthermore, most (74.6%) of the boat passages in the MPA occurred at a reduced distance from the coast (<250 m), generating greater disturbance to ospreys (Appendix S3).

At sites located along these boat trips, nautical traffic significantly impacted osprey behaviour (Fig. 5). There, the number of disturbing events per hour was higher, with females at the nest spending more time alarming for approaching boats, and fewer prey-items were brought back to the nest by males (Fig. 5). In this context, time spent alarming or repeatedly flying off the nest may reduce time allocated to other important activities (notably foraging).
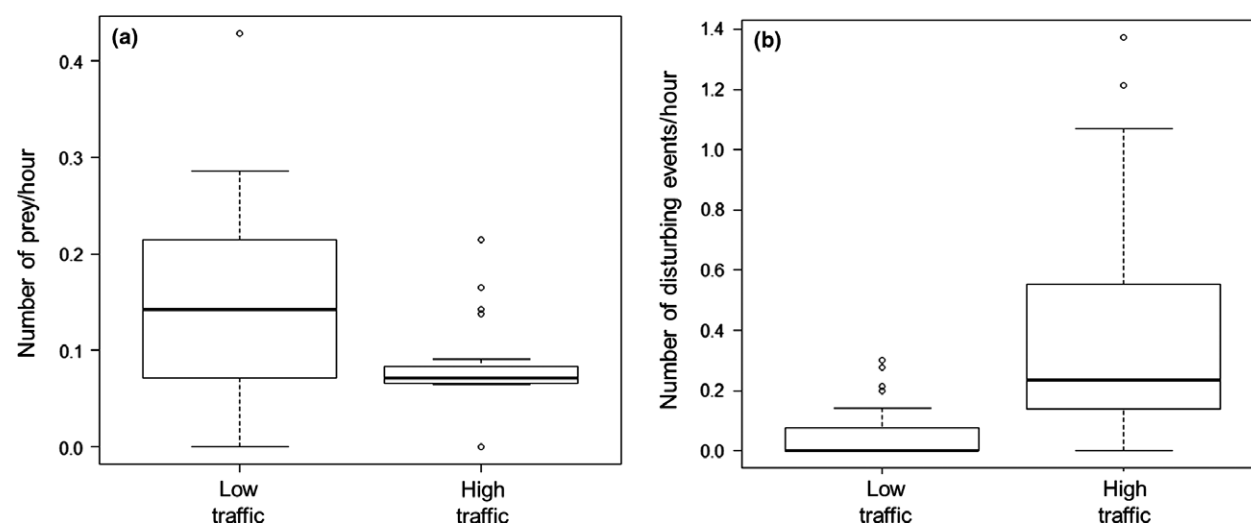

Figure 5 (a) Number of prey items brought to the nest per hour by male ospreys and (b) disturbing events per hour in 'low-traffic' and 'high-traffic' areas in Corsica.
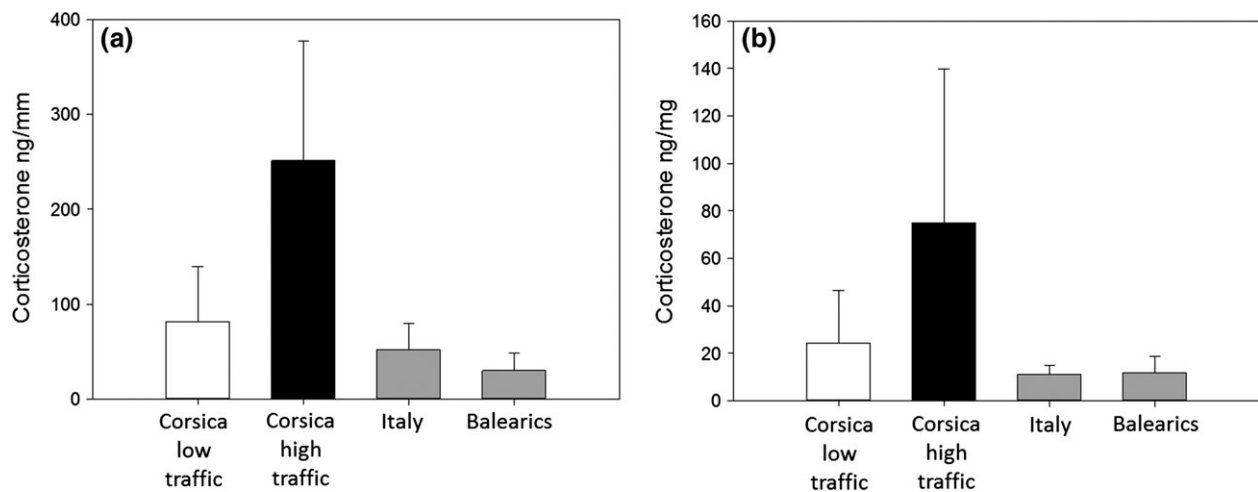
Figure 6 Mean values of (a) corticosterone temporal expression (ng/mm) and (b) its concentration (ng/mg) for each locality. Corsica has been split in low- and high-traffic areas (respectively white and black bars); other control sites (Italy and Balearics) in grey bars.

Furthermore, boats approaching too closely can scare parents off the nest, which results in eggs or chicks being left unattended which may favour attacks by predator like Yellow-legged gulls *Larus michaellis* or Ravens *Corvus corax* (Bolduc & Guillemette, 2003). Nautical traffic may also have further perturbing effects. In particular, epipelagic fish that constitute the main food source for ospreys may change behaviour, by switching daily activity patterns or by swimming deeper to avoid noise (Bracciali *et al.*, 2012). One may also speculate that boat traffic may enhance the vorticity of surface water, perturbing the epipelagic area upon which ospreys are critically dependent for efficient foraging. Confronted with such perturbed foraging areas, ospreys may move away in search for calm waters, spending more time travelling; this may also result in lower rates of food provisioning to the nest, and in lower reproductive performance.

This hypothesis is supported by the fact that chicks from nests exposed to boat traffic had significantly higher corticosterone levels, indicating physiological stress. This is predicted to have a negative effect on chick growth and survival rates. Human recreational activities have already been identified as the cause of physiological stress impacting individual fitness. For example, stress hormone levels increased markedly for individuals living close to human recreational areas in Capercaillie *Tetrao urogallus* and Hoatzin *Opisthocomus hoazin* (Müllner, Eduard Linsenmair & Wikelski, 2004; Thiel *et al.*, 2011). However, with our correlative approach, we cannot attribute with certainty the observed pattern of corticosterone accumulation due to boat traffic. Multiple factors can act concurrently to determine stress responses. For example, higher concentrations of corticosterone could result from the presence of potential predators in the surroundings and/or by conspecific intrusions in the territory of their parents: in these cases, a stressed female may effectively increase his chick stress levels (Bretagnolle & Thibault, 1993). Another cause of stress could be lower food delivery and nutritional stress. Indeed, former studies showing elevated corticosterone levels in response to stress suggested that birds are thereby able to physiologically cope with food shortages associated with unpredictable food resources (Love, Bird & Shutt, 2003).

Management implications

Ecotourism is a notable source of environmental disturbance (Buckley, 2004). A global analysis of marine reserve regulations at 91 MPAs across 36 countries found that a majority of high-risk activities involved motorized boats (Thurstan *et al.*, 2012). When designing MPAs, anticipating forthcoming touristic fluxes is therefore essential to avoid facing acute management crises as in the case of Scandola MPA. Such anticipatory planning necessarily involves pertinent socio-economic factors analyses (Badalamenti *et al.*, 2000) leading to a consensual regulation of public access and ship traffic. Furthermore, the designation of MPAs must be complemented by a sound management plan, and the allocation of the financial means necessary to its enforcement. Tourism in Corsica actually started in the early 20th century and, based on observed numbers, predictions of current trends have been made: such previous studies already indicated that enhanced ecotourism and related boat traffic may affect marine biodiversity at Scandola in the longer term (Francour, 1994; Francour *et al.*, 2001; Richez & Richez Battesti, 2007; Tavernier, 2010).

We strongly feel that an improvement of osprey conservation within the Scandola MPA will only be possible through a collaboration with the local tourism industry. This might be facilitated by the fact that the Regional Natural Park of Corsica is increasingly aiming towards sustainable tourism development, to enhance the value of local biodiversity while reinforcing the sanctuary status of its UNESCO World Heritage Site. In this framework, Scandola has a great potential for achieving both goals, yet disturbance caused by enhanced boat traffic has to be carefully managed.

Our integrative study is a major incentive for a better integration of terrestrial and marine conservation processes, to achieve an improved protection of coastal biodiversity on a worldwide scale. Identifying long-term effects of established MPAs upon wildlife is of crucial importance for setting conservation priorities within coastal areas, especially in human-dominated marine ecosystems (Sala *et al.*, 2002). Robust scientific evidence of anthropogenic stress exerted upon species living within MPAs stresses the worldwide importance of rigorously implementing sustainable ecotourism. It is essential that such evidence drives MPA design and management, to guarantee their long-term efficiency.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Prey resource availability (methods and results).
Appendix S2. Home ranges and feeding areas of breeding ospreys (methods and results).
Appendix S3. Tourism and boat traffic evaluation (methods and results).
Appendix S4. Corticosterone analyses (methods and results).
Appendix S5. Complementary info on demographic data analyses and behavioural parameters analyses.

COMMENTARY

Long-term study highlights the conundrum of nature-based tourism in marine protected areas

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Historically, protected areas (PAs) have been designated in areas that are either of low productivity (i.e. not suitable for agriculture, pastoralism or urban development) (Joppa & Pfaff, 2009) or more recently due to the presence of iconic species or landscapes. In a world of rapidly changing landscapes, where natural environments are becoming challenging to access for an increasingly urbanized human population, PAs offer people the chance to experience intact nature. Also, they often provide a mechanism to fund conservation of those landscapes (Buckley *et al.*, 2012; Steven, Castley & Buckley, 2013; Buckley, Morrison & Castley, 2016), although this positive outcome can be offset by the negative impacts associated with increased visitors in PAs (Steven, Pickering & Castley, 2011; Steven & Castley, 2013). Marine protected areas (MPAs) present a heightened challenge for natural area managers, given the often ambiguous tenure and jurisdictional context in which they occur, as well as the simple fact that they cost more to physically monitor (i.e. maritime infrastructure and their associated costs).

In this study, Monti *et al.* (2018) have explored a specific case of this much broader issue, using a multifaceted approach illustrating the negative effects tourism can have on resident ospreys *Pandion haliaetus*. They focus on the island of Corsica, France, which lies in the Mediterranean Basin Biodiversity Hotspot (CEPF 2018). In a refreshingly holistic approach, the authors undertake to assess the population level as well as the behavioural, ecological and physiological effects tourism is having on the ospreys in the Scandola MPA in Corsica. Such a comprehensive effort supports the presented conclusions about the drivers and influencers of osprey presence and abundance in the MPA. Additionally, their population assessments draw on data spanning 37 years. This represents at least three generations of ospreys in the area.

The findings of Monti *et al.* (2018) provide justification for concerns about the sustainability of tourism in the UNESCO listed Scandola MPA. Despite confirming adequate prey resource availability for ospreys in the MPA, relative to outside the MPA, the species' breeding performance is in decline. By monitoring the ospreys' behaviour and employing physiological tests assessing stress levels, Monti *et al.*, (2018) found that disturbance by tourist boats is more than likely to blame for this decline. The authors observed significantly higher rates of alarm behaviour and associated disturbance events at sites with increased tourism-related boat traffic. These responses reduced the ospreys' ability to provide resources for their offspring, where fledging and overall breeding success were both significantly reduced inside the MPA (where the bulk of tourism occurs) relative to outside the MPA. Finally, *Monti et al.,* (2018) provide evidence that the flushing of adult ospreys from nests at sites with high boat traffic is likely increasing the stress responses in the chicks left unattended in the nests. Chick feather samples from areas of high boat traffic exhibited higher levels of the stress hormone corticosterone compared to those from elsewhere in Corsica. This additional step supports the authors' case for the negative effects of tourist boat traffic on ospreys.

The impacts of tourism on threatened birds in the Mediterranean Basin Hotspot have been illustrated previously (Steven & Castley, 2013). Unlike the threats faced by many biodiversity hotspots in developing countries, Steven & Castley (2013) suggested that the negative effects of tourism in the Mediterranean could be managed. Given the relatively advanced economies of the region, these countries would have the capacity to invest in practices that enhance sustainable tourism. This study by Monti *et al.* (2018) provides further justification for this, by highlighting these negative effects on one of Europe's most iconic raptors, the osprey. Given the perilous status of this species elsewhere in the region, these findings should certainly be viewed as the warning signal that something needs to be done.

Unfortunately, this study does not distinguish between the many types of tourism that are no doubt taking place within the Scandola MPA. Describing the intense tourism-related

boat traffic as 'ecotourism' is possibly erroneous, given the common definitions applied to the use of the term (i.e. net benefits for both the social and environmental as well as economic interests). It could be argued that the activities described in this paper, while certainly nature-based, are probably not ecotourism, as the authors refer to it at several points in the study. Without getting too waylaid in definitions, it is prudent to keep in mind what we, as researchers and often critics of industrial players, are truly assessing. Applying terms like ecotourism to generic nature-based tourism operations is unfair to those operators that do ensure their activities are sustainable and that their negative impacts are mitigated, or at the very least minimized.

In conclusion, Monti *et al.* (2018) have provided a clear message that the current tourism practices in the Scandola MPA are having deleterious effects on an iconic species, if not other species as well. They have tested hypotheses using a multidisciplinary approach, ensuring that their findings are not communicated in the absence of a comprehensive assessment. The lessons learned from this case study and that of others focusing on this iconic species (Shiel, Rayment & Burton, 2002; Dickie, Hughes & Esteban, 2006) should provide the motivation needed to take action for the European osprey. Studies such as this can form the basis for well-informed management plans, upon which political support can be sought to enact planning policies that ensure the ecological and economic sustainability of these natural areas.

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COMMENTARY

Satellite factors influencing the impact of recreational activities on wildlife

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The reading of Monti *et al.* (2018*a*) has brought to my mind several issues that may be worth considering in relation to present and future human/wildlife coexistence. First, it made me think of how fine-grained conservation has become in the 21st century. Only a few decades ago bears, wolves, otters, whales or birds of prey (to name a few) were still being killed by active human persecution. However, the change in attitudes towards predators has been so great (see Martínez-Abraín *et al.*, 2008*a*) that our present concerns spin around preventing any type of discomfort to our respected study models. One of the sources of likely human disturbance is outdoor recreational activities. The effect of these activities on wildlife is a topic that has resisted quantitative systematic review (see Martínez-Abraín *et al.*, 2010) and hence further information is welcome. The correlational evidence provided by Monti *et al.* (2018*a*), linking the frequency of boat passages within 250 m of osprey nests with reduced breeding performance inside the Scandola MPA (Corsica) but not outside, is quite convincing, despite the existence of some alternative explanations (i.e. density-dependence), as stated by the authors.

However, one must remember that the osprey is a long-lived species and that the geometric growth rate of long-lived species is much more sensitive to survival than to reproduction. That is, the Corsican population is not going to be seriously jeopardized because of a reduction in breeding performance. It is in fact the largest osprey population in the Mediterranean, and has increased from only three pairs in the 1970s to 34 pairs in 2011 (Monti *et al.*, 2018*a*). Hence, I think that concerns about decreased breeding success are more of an ethical issue than a biological one. I agree that 21st century conservation needs to be that ethical and fine-grained, but it is also good to keep in mind where we come from and how fast the change in attitudes has been, especially in southern Europe.

In addition, we take for granted that the Mediterranean populations of ospreys are characterized by being sea-cliff nesters, and this habit is commonly attributed to their use of the marine environment for hunting (Monti *et al.*, 2018*b*).

However, we recently suggested (Martínez-Abraín, Jiménez & Oro, 2018) that facultative tree/cliff nesting raptors use cliffs currently as a consequence of intense past human persecution, rather than because of preference. From this perspective, osprey populations in central/northern Europe would nest mainly in trees because they were not so intensively persecuted in the recent past. Hence, tree-nesting could actually be independent of hunting in freshwater lakes. In this sense, our prediction is that most facultative cliff-nesting raptor species will increasingly shift to trees for nesting in the near future, and that this may have positive demographic consequences for them, because the limiting factor of availability of high-quality cliffs will vanish. We have shown that some large raptor species such as golden eagles, Bonelli's eagles or booted eagles are already doing that in Spain (Martínez-Abraín *et al.*, 2018). This will most likely happen as well with osprey. In fact, some bold osprey pairs have already started this shift at the Balearic Islands, nesting in pine trees close to urbanized areas (J. Muntaner, pers. comm.), and some osprey pairs already use Spanish reservoirs (Ferrer & Morandini, 2018). Centuries-old human persecution selected for shy individuals that are afraid of humans and nest in inaccessible places, but the lack of persecution during the last 60–70 years is starting to change things, bringing in new wildlife. It is well known that flight initiation distances in colonies of social birds are smaller in highly visited colonies, provided that people are respectful of wildlife (see Martínez-Abraín *et al.*, 2008*b*). Genetically bold and/or culturally habituated eagles will be less reluctant to coexist with people in close proximity if the trend of peaceful coexistence continues. Hence, the bold/shy nature of individuals could be very informative for the current debate on the suitability of translocating osprey chicks from northern to southern European populations (Ferrer & Morandini, 2018). This is so because northern chicks could bring bold genes to Mediterranean populations, accelerating the loss of fear towards humans.

It is also worth remembering that, according to Gill, Norris & Sutherland (2001), the degree of disturbance of

human activities on wildlife is inversely proportional to the amount of alternative habitat available for the individuals to move to when disturbed. In a similar study to that of Monti *et al.* (2018*a*) we found, 16 years ago, that the rise in tourist boats did not affect the overall number of breeding pairs or the productivity of Eleonora's falcons nesting in the small Columbretes archipelago (a marine and terrestrial reserve in the western Mediterranean). However, the human disturbance caused a shift in the degree of occupancy of the volcanic islets by the falcons, favouring the islets with lower human presence close to colonies (Martínez-Abraín *et al.*, 2002). The birds solved the problem by shifting spatially because they had the option to do so. Moreover, some authors have found that *a priori* negative human impacts (such as the construction of an airport or a wind farm) have forced some small social raptor populations (Montagu's harriers and griffon vultures) to abandon their comfort zones, and that this has unexpectedly had positive consequences for the species via dispersal to high-quality but still empty sites (Oro, Jiménez & Oro, 2012).

Finally, it is also relevant to keep in mind that often negative human impacts occur only in interaction with some other ecological agent, rather than operating alone. In a classical example, Sergio *et al.* (2004) reported that corvids had negative effects on the neighbouring peregrine falcons in the Italian Alps only when humans had recently passed by the nests and the incubating birds had left them unprotected. The same interaction can be pictured from the opposite perspective. Human impact on nesting birds often only results in negative consequences if this effect interacts with an ecological factor, such as the presence of an egg/chick predator close to the nests. Importantly, the abundance of facultative opportunistic predators (e.g. large gulls or ravens) could have been in turn favoured previously by the availability of fishing discards or garbage dumps in the proximity of colonies due to humans. Hence, the direct effect of tourist presence will only have negative biological consequences if the indirect human effect has predated that of tourists and it is mediated by the presence of subsidized opportunistic consumers (Oro *et al.*, 2013). In summary, we may need new conservation strategies and policies for new wildlife, within a new social context of pacific coexistence with wildlife, for the future. Let's keep that in mind.

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RESPONSE

Conserving wildlife facing mass-tourism calls for effective management

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We thank Drs Steven and Martinez-Abrain for elaborating on problems related to tourism impacting endangered bird species. In the 21st century, nature-based tourism has often reached the magnitude of mass-tourism. Even if it generates substantial revenues which may contribute to enhanced conservation, this industry is based on finite resources, such as accessible places rich in scenic beauty or charismatic wildlife (Steven, Pickering & Guy Castley, 2009). This is very much the case for the UNESCO site of Scandola, the focus of our study. Until the late 1990s, boat traffic within the reserve operated on a small scale for limited numbers of visitors, mainly naturalists. At that time, preliminary studies had already pointed out the risk that future enhanced ecotourism and related boat traffic would have affected marine biodiversity at Scandola in the long term (Francour, 1994). More recently, traffic in this area has been increasing exponentially, concomitant with a decrease in the environmental awareness of the visitors. This pattern is also visible at the scale of Corsica, with dire environmental consequences for the natural heritage of this sensitive Mediterranean island. Overall, we agree with Dr Steven (2018): Scandola is no longer an ecotourism destination because of the degradation of the status of its flagship species, the emblematic Osprey.

Dr Martinez-Abrain (2018) argued that Corsican ospreys, being long-lived birds, may not be seriously threatened because a reduction in their current breeding performance may not necessarily impact population viability. Indeed, the number of osprey pairs in Corsica and within the Scandola reserve has remained stable across 2010–2018, at respectively 27.2 and 5.4 pairs each year. Yet, as recently shown by Genovart, Oro & Tenan (2018) in other long-lived birds, if adult survival remains constant, other demographic traits such as fecundity or immature survival may then drive population size. Between 2010 and 2018, the osprey breeding success was 0.72 fledglings per nest in Corsica and 0.29 in Scandola. Using matrix population models developed by Wahl & Barbraud (2014) on the osprey, with survival estimates for continental France (Wahl & Barbraud, 2014) and a reintroduced population in Italy (Monti et al., 2014), we found that all deterministic and demographic stochasticity models yielded population growth rates with a lambda <1 (range 0.938–0.985), indicating population declines. Simulations with demographic stochasticity for six pairs in Scandola yielded extinction probabilities of 0.478–0.854 within 50 years, depending on the survival rates. To obtain a population in numerical growth ($\lambda > 1$), using Italian osprey survival rates, it would be necessary to increase juvenile survival from 0.20 to 0.40, or breeding success from 0.72 to 1.4 fledglings per nest (unpublished results, available upon request to the authors). Because juvenile mortality mainly occurs during migration and wintering in North Africa (Monti et al., 2018a), where conservation is difficult to promote, actions should rather focus on increasing breeding success in Corsica, to reach 1.5 fledgling per nest, which was the average before 2010. Therefore, the observed decrease in breeding success is both an ethical and a biological issue.

Regarding the adaptability of ospreys with respect to human disturbance, we agree that there might be regional differences. On this scale of sensibility, Corsican ospreys rate high, and we speculate that this might be due to intense persecutions to which they have been exposed in the past. Such particularism should also be taken into account when designing adequate conservation actions for the genetically unique Mediterranean population.

Nest site selection by ospreys may be affected by human activities: in many places in the world, ospreys build their nests on man-made structures (Washburn, 2014). However, it is questionable to use the argument of osprey behavioural plasticity to justify perturbation of the rocky coastal habitats to which they are tightly linked for reproduction. In this context, a comparison with ospreys from Andalucía does not hold, because Andalusian birds were translocated from northern Europe (Muriel et al., 2010), from forested areas where ospreys mostly find their food in lakes, contrary to the indigenous Mediterranean birds. In an accompanying paper (Monti et al., 2018b), we emphasized the importance of considering the origin of the birds prior to translocation, and stressed that north-European and Mediterranean ospreys are genetically distinct. The migratory habits of these two

populations are also markedly different (Monti *et al.*, 2018*a*). Hence, we strongly disagree with the viewpoint by Ferrer & Morandini (2018) that Dr Martinez-Abrain (2018) cites as an example. The translocation of numerous birds from northern to southern Europe is not recommended and contradicts modern approaches of conservation genetics, since it would completely homogenize the species at European level, hindering the possibility to preserve the natural genetic diversity of the Mediterranean population.

Overall, vanishing ospreys provide strong warning signals about the general degradation of the marine environment within Scandola: in 2018, no less than 523 boats visited the reserve each day, and a long-term study demonstrated a 60% local decrease since 2012 in the abundance of emblematic fish species, such as dusky groupers *Epinephelus marginatus*, brown meagres *Sciaena umbra*, or white seabreams *Diplodus sargus* (Groupe d'Etude du Mérou, unpubl data). Such warning signals call strongly for a regulation of boat traffic: boats should stay at least 300 m away from osprey nests to avoid any disturbance to parents and offspring and to let the males fish efficiently. To delimit off-limits areas, waypoint buoys could be placed at sea according to the ospreys' active nest distribution. Enlarging reserve boundaries would dilute disturbance: this measure has been requested by the Parc Naturel Régional de Corse for many years. Surveillance should also be conducted around all osprey nesting sites, and it might be envisaged to visit Scandola only between August and March, outside of the osprey breeding season. Such measures have already proved efficient at other marine protected areas for the restoration of bird and fish communities (Velando & Munilla, 2011), often with the support of local stakeholders (Badalamenti *et al.*, 2000).

In a wider context, we agree with Dr Martinez-Abrain (2018) with respect to the necessity of designing what he calls "new conservation", yet with a slightly different angle: we strongly feel that wild nature should be protected for what it is, and not only in the context of its coexistence with humans (Wuerthner, 2014).

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Supporting Information

Appendix S1: *Prey resource availability (Methods and Results)*

We assessed prey availability to ospreys at 24 sites hosting osprey nests along the west coast of Corsica (8 sites inside and 16 sites outside the MPA; Fig. 1a). Surveys were performed twice each year at each site, and the monitoring protocol was repeated in 2012 and 2013, yielding a total of 96 sampling sessions.

The subsurface area (0-2m depth), which corresponds to the osprey feeding horizon, was filmed with a HD-Hero 2 GoPro camera (USA) attached below the bow of a kayak, set with a wide angle of 170° to scan a field of approximately 3 m left/right. Transects were composed of 4 stretches of 100 m parallel to the coastline, set at 20, 40, 60 and 80 m away from the shoreline (Fig. 1c-1d). Each transect was pre-recorded on a GPS, which allowed the paddler to maintain constant headings and speed (ca. 5 km.h^{-1}). Transects were performed during the osprey breeding season (in June and July), during daylight and on calm days, to optimize viewing conditions and mimic osprey foraging conditions (as ospreys usually do not hunt at sea when conditions are harsh; Thibault *et al.*, 2001). We used a Secchi disc to control water turbidity and to ascertain good visibility conditions before each transect.
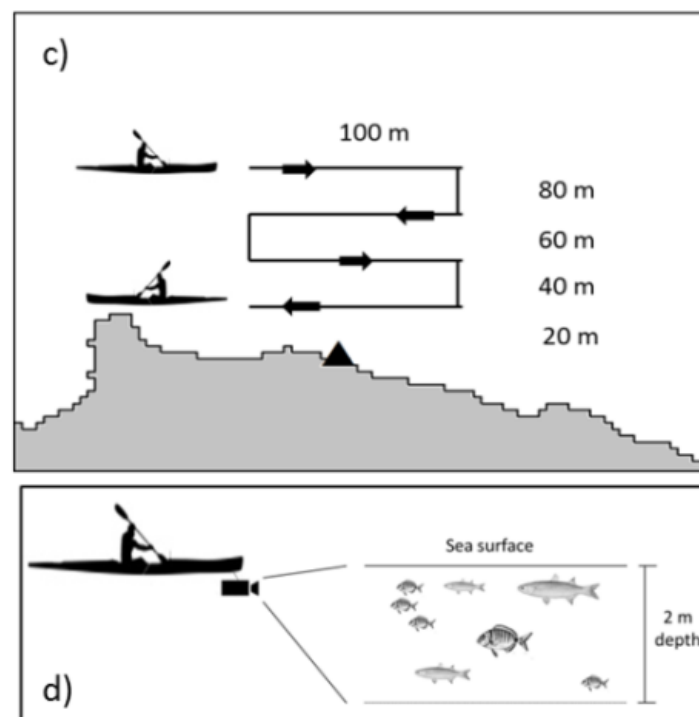

Fig. 1 c) structure of the transect for fish video recording from a kayak; d) simplified view of the water column recorded by the camera attached to the bow of the kayak.

Video recordings were inspected by two observers (FM and another person) to minimize errors in fish species identification and counting. Each fish was identified following Louisy & Trainito (2010). Since objects appear 4/3 larger in water than in the air (Ross & Nawaz, 2003), we performed preliminary tests using fish models of different sizes to calibrate fish sizes estimates. To further limit such errors, we used five size classes (1 = <10 cm; 2 = 10-20 cm; 3 = 20-30 cm; 4 = 30-40 cm; 5 => 40 cm). To estimate biomass from underwater length observations we used the following formula: $W = aL^b$, where W is mass in grams; L is the standard length in centimetres and a and b are constants, following Morey *et al.* (2003). For each transect we calculated the following parameters: a) total number of fish; b) total fish biomass (g); c) density index (total number of fish per m transect); and d) the total number of fish >20 cm per transect. For data analyses all parameters were log+1 transformed to achieve normality; sites were ranked as 0 (outside reserve) and 1 (inside reserve). We used general linear models (GLM) to test between-year effects (2012 vs 2013). We then ran GLMM including 'year' and 'transect' as random effects and log of biomass, log of number of fish and log of density index as dependent variables.

Fish biomass, fish numbers and density followed a Gaussian distribution after a logarithmic transformation (Shapiro-Wilk normality test: Log_Biomass, $W=0.94$ $p<0.0001$; Log_Number of fish, $W=0.96$ $p<0.0001$; Log_Density Index, $W=0.69$ $p<0.0001$). There were no significant differences between 2012 and 2013 for the three parameters: Log_Biomass (GLM: $F_{1,93} = 0.426$, $p=0.515$), Log_Number of fish (GLM: $F_{1,93}=0.0$, $p=0.991$), Log_Density Index (GLM: $F_{1,93}=1.17$, $p=0.281$). We therefore pooled data across years. Our models showed a strong reserve effect, and the three parameters considered were not affected by random effects such as transect and year repetitions. The MPA hosted a larger number of fish (Log_Number of fish: $F_{1,96} = 0.38$, $p = 0.016$) and a higher total biomass (Log_Biomass: $F_{1,96} = 0.90$, $p = 0.001$) compared to sites located outside of the MPA (Fig. a), although the density index was not significantly higher (Log_Density Index: $F_{1,96} = 0.005$, $p = 0.617$). Furthermore, inside the MPA, large fish (> 20 cm) tended to be more abundant (MPA = 6.12 ± 11.2; outside = 1.9 ± 8.9 number of fish).
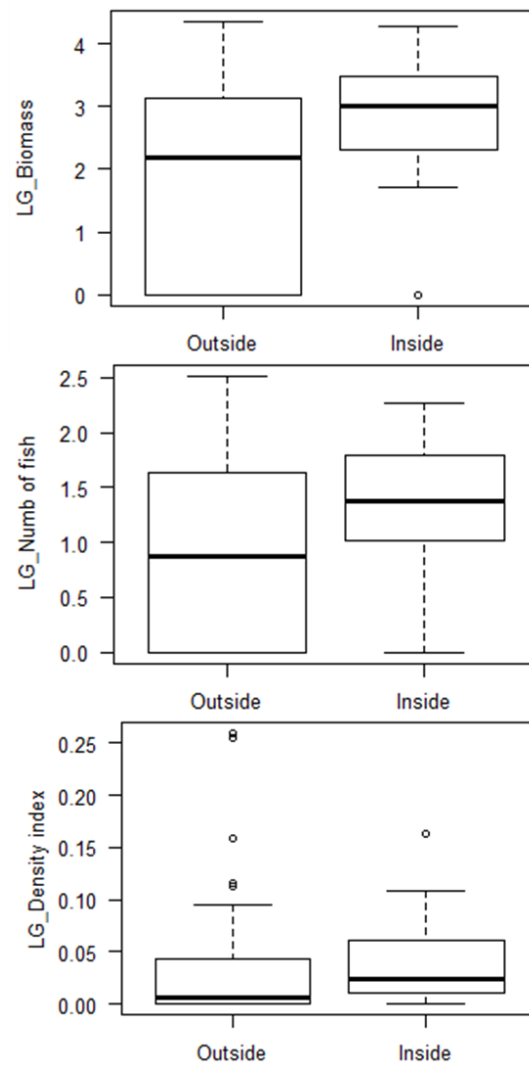
Fig. a Mean values of biomass, number and density index of fish (expressed as Log normal function) for transects located inside and outside of the MPA.

Appendix S2: *Home ranges and feeding areas of breeding ospreys (Methods and Results)*

Foraging home ranges of 9 breeding adult ospreys (2 males and 7 females) were determined by GPS tracking. Birds were trapped at nests before the beginning of the breeding season (early March 2012 and 2013) and fitted with a GPS/GSM tag (Duck-4 model, ECOTONE, Poland, 35 x 55 x 15 mm, 24 g ~ 1.5% of body mass). Devices recorded one fix every 30 minutes across the entire breeding season (March-July). Since parental care and nest attendance is performed by both parents during incubation and chick rearing (Poole, 1989), we defined as failures any abrupt abandonment of the nesting site. In case of breeding failure, atypical ranging movements performed by birds were excluded from home range analyses. Thus, home ranges were calculated only during effective breeding activities. We used a fixed kernel density estimator (Worton, 1989), with Hawth's Tool extension in ArcGis v9.3.2 (www.esri.com) to calculate 95% foraging home ranges (UD95%) and 50% core foraging areas (UD50%). GPS tracking data can be consulted in Movebank (www.movebank.org; project name: Osprey in Mediterranean (Corsica, Italy, Balearics)).

Home ranges estimated during the breeding season showed that the feeding areas of adult ospreys were concentrated along the coast. Ospreys never ventured offshore to fish (median distance from the coast = 0.012 km, range: 0-3.2 km), but rather remained in the surroundings of the nesting sites, fishing in marine coves. Mean individual foraging home range was 64.05 ± 59.54 km^2 and mean core feeding area 5.5 ± 3.57 km^2 (Tab. a). Exploratory foraging trips were performed by ospreys along rivers and interior lakes when sea conditions were harsh for an extended period (Fig. a).

Table a: Estimates of core foraging areas (UD50%) and foraging home ranges (UD95%) of adult ospreys tracked by GPS in Corsica.

| ID	Sex	Year	Monitoring Period	UD50% (km²)	UD95% (km²)
A02	M	2012	24/03-21/04	10.79	183.28
A03	F	2012	27/03-30/04	4.94	56.46
FOSP01	F	2013	27/03-30/06	4.01	32.16
FOSP02	F	2013	17/03-24/05	13.88	183.66
FOSP03	F	2013	23/03-28/05	9.13	94.94
FOSP04	F	2013	23/03/03/04	4.55	28.97
		2014	25/03-20/04	3.93	22.07
FOSP05	M	2013	27/03-24/06	4.11	77.17
		2014	06/02-30/06	4.15	50.43
FOSP06	F	2013	29/03-07/05	5.29	71.82
		2014	24/03-25/06	2.30	11.83
FOSP08	F	2013	05/04-24/06	2.23	9.88
		2014	09/03-08/07	2.22	10.01
Mean				5.50	64.05
SD				3.57	59.54
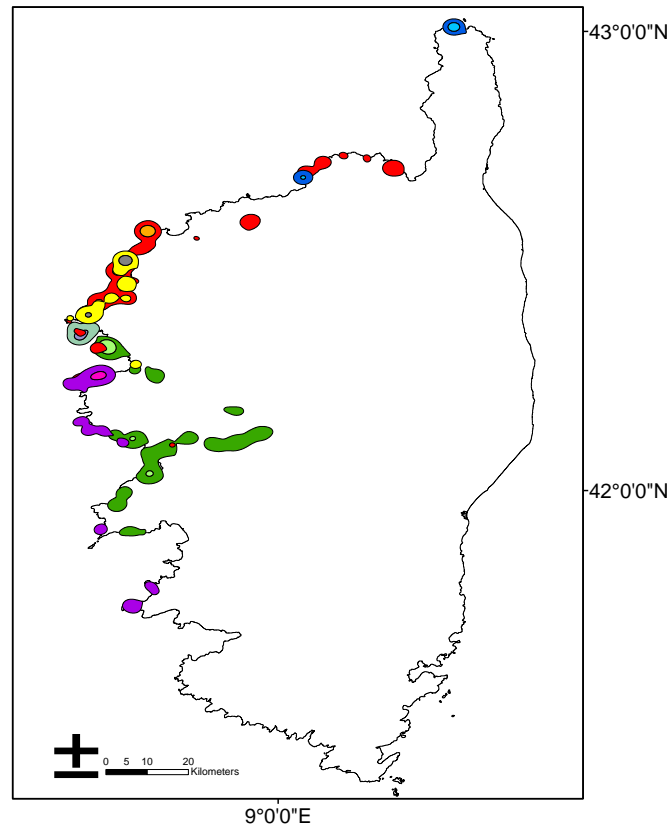
Fig. a Foraging home ranges (fixed kernel at 95%) and core foraging areas (fixed kernel at 50%) with darker and lighter colours respectively: each colour represents one of the 9 adult ospreys monitored during the breeding season in Corsica.

Appendix S3: *Tourism and boat traffic evaluation (Methods and Results)*

We carried out two specific censuses in 2013 and 2014. In 2013 we assessed the at-sea distribution and frequency of boat passages within the MPA, as well as the distance of boat to the shore (in 2 classes: 0-250 m; >250 m), because ospreys are systematically disturbed by approaching boats at distance <250 m (Bretagnolle & Thibault, 1993). Two land-based vantage-points, located at the northern and southern limits of the MPA were used to monitor entrances and exits of boats. The same observations were performed within a control area (Revellata) outside of the MPA with a similar density of osprey nests. Both areas were located between two harbours from which tourist boats departed (Fig. 1b). Two observers worked simultaneously in each area between 9:00-17:00 during 4 observation-days (two days during the second half of June 2013 and two during the first half of July 2013). We selected this period because it corresponds to osprey chick-rearing, during which disturbance is critical for this species (Poole, 1989).

In 2014 the number of boat passages at osprey nests was recorded while studying the behaviour of breeding pairs (see details below). In this case, distance categories considered for boat passages were a) 0-100 m and b) 100-250 m, to focus on boats which were more likely to disturb ospreys.

The number of tourist shuttles operating inside the Scandola MPA and their passengers transport capacity increased from only 3 ships transporting c. 200 persons per day in 1977 to 32 ships transporting c. 2,200 persons per day in 2010 (Richez & Richez Battesti, 2007; Tavernier, 2010; Fig.a). However, data were not available for each year during the study period. Therefore, we extracted the total annual number of tourists visiting Corsica between 1986-2014 using data from the Observatoire régional des transports de la Corse (www.ortc.info;). A strong positive relationship was found between the annual number of tourists visiting Corsica and the number of shuttles working within Scandola (Spearman rank correlation: $rs_{(12)} = 0.963$, p <0.001, Fig. b).

We therefore used this relationship to estimate the yearly transport capacity of touristic shuttles in Scandola for the study period (see also Fig. 4).
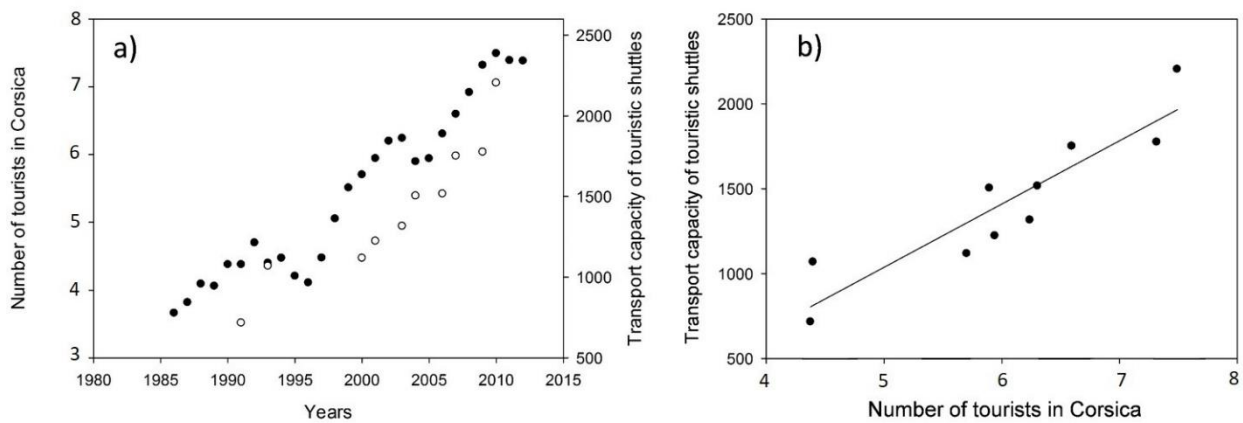
Fig. a Historical trends of total annual numbers of tourists (millions) visiting Corsica during 1986-2012 (black dots; data extracted from: http://www.ortc.info) and of the transport capacity of tourist shuttles operating in the Scandola MPA (open dots; data extracted from Richez & Richez Battesti, 2007; Tavernier, 2010);

Fig. b Linear regression between annual estimates of number of tourists in Corsica and daily number of visitors in the MPA.

The total annual number of tourists visiting Corsica increased consistently, from c. 3.6 millions in 1986 to c. 7.5 millions in 2013 (Fig. a). Our census conducted in 2013 showed that the number of boats visiting the MPA each day was twice that recorded within the control area outside of MPA (Fig. c). In both cases, numbers almost doubled between June and July (Fig. c). Further, >3 times more boats approached the coastline <250 m inside MPA compared to the control area (Fig. c). The number of boats passing at a distance >250 m from the coast was similar between the two areas in both months (Fig. c).

In 2014, the number of boat passing close to osprey nests (<250 m) was significantly higher for nests located inside the MPA than for those outside (GLMM: $\chi^2_{1,147} = 10.484$; p = 0.001), especially when considering those passing at <100 m (GLMM: $\chi^2_{1,147} = 15.95$; p = 0.001).
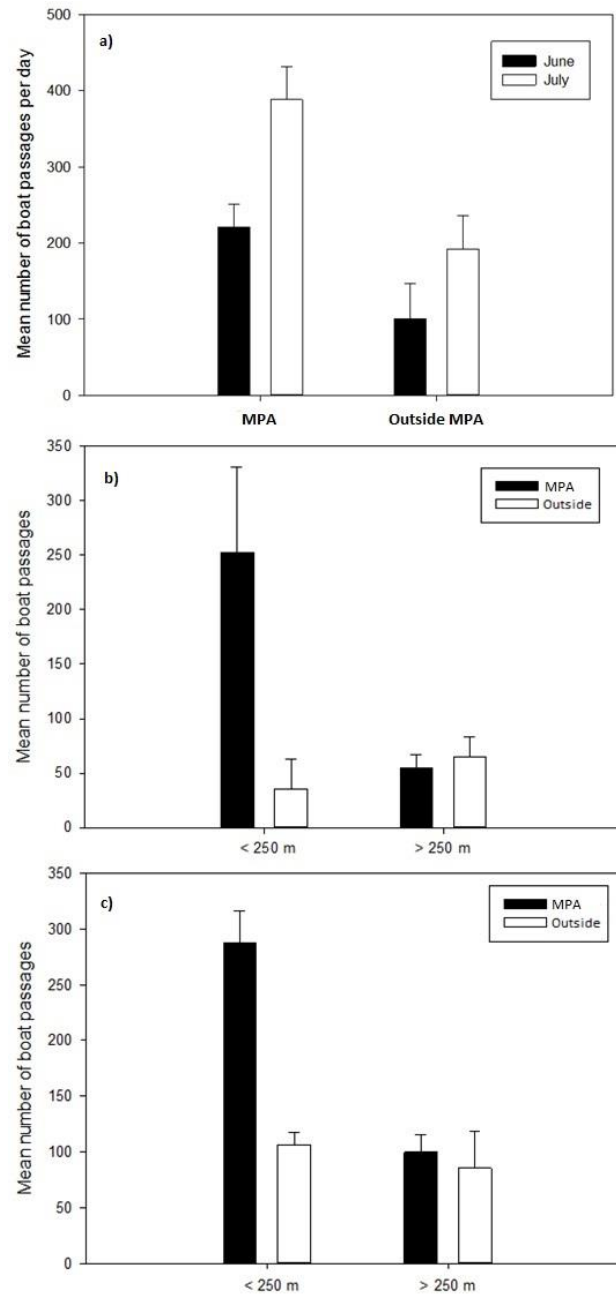
Fig. c Boat traffic during summer in Corsica: a) mean number of boat passages per day in June and July for sites inside and outside of the MPA. b) and c): mean number of boat passages per day < 250 m and > 250 m from the coast in June and July, respectively.

Appendix S4: *Corticosterone analyses (Materials and method)*

Feathers were stored in paper envelopes before analyses, during which we extracted corticosterone following Bortolotti *et al.* (2008). Before removing the calamus we measured the length of the feather. Feathers were then cut into pieces < 5 mm^2 and placed in 16 x 100 mm glass tubes. Three glass beads and 10 ml methanol (HPLC grade) were added and the tubes were placed into an ultrasonic waterbath for 30 min and then at 50° C overnight. The methanol mixture was filtered through filter paper placed on a glass funnel. The methanol extracts were collected in tubes placed in a 50° C waterbath until dry. Feather extracts were then redissolved in 200ul steroid dilution of the ICN I^{125}radioimmunoassay kit (Cat. #07-120102; ICN Biomedicals/MP Biomedicals, Solon, Ohio; USA) for measurements. We followed the protocol of the company with modifications as described in Washburn *et al.* (2002): the volume of all reagents was halved; the dilution of the samples was performed at 1:50 instead of 1:200. The standard curve was extended by 2 points.

Appendix S5: *Complementary info on demographic data and behavioural parameters analyses*

a) Results of model selection of GLMM on the effects of the MPA and time on components of reproductive parameters on Corsican ospreys. Selected models are shown in bold.

Response variable	Model	Variables retained	K	logLik	AICc	ΔAICc	Weight
N eggs laid (541)	**1**	**Null**	**4**	**-815.09**	**1638.25**	**0.00**	**0.50**
	2	time	5	-815.03	1640.17	1.93	0.19
	3	Out/in MPA	5	-815.04	1640.19	1.94	0.19
	4	time+Out/in MPA	6	-814.98	1642.12	3.87	0.07
	5	time*Out/in MPA	7	-814.29	1642.80	4.55	0.05
N eggs hatched (730)	**1**	**time*Out/in MPA**	**7**	**-1181.01**	**2376.18**	**0.00**	**0.31**
	2	**Null**	**4**	**-1184.13**	**2376.31**	**0.14**	**0.29**
	3	Out/in MPA	5	-1183.51	2377.09	0.92	0.20
	4	time	5	-1184.01	2378.10	1.92	0.12
	5	time+Out/in MPA	6	-1183.40	2378.92	2.74	0.08
N chicks fledged (744)	**1**	**time*Out/in MPA**	**7**	**-1054.62**	**2123.40**	**0.00**	**0.99**
	2	time	5	-1062.52	2135.13	11.73	0.00
	3	time+Out/in MPA	6	-1061.53	2135.18	11.78	0.00
	4	Null	4	-1064.12	2136.29	12.90	0.00
	5	Out/in MPA	5	-1063.17	2136.41	13.01	0.00
Hatching success (538)	**1**	**time*Out/in MPA**	**7**	**-283.10**	**580.42**	**0.00**	**1.00**
	2	Null	4	-283.10	593.00	12.58	0.00
	3	Out/in MPA	5	-292.15	594.42	14.00	0.00
	4	time	5	-292.37	594.86	14.44	0.00
	5	time+Out/in MPA	6	-292.06	596.28	15.86	0.00
Fledging success (576)	**1**	**time**	**5**	**-332.80**	**675.70**	**0.00**	**0.40**
	2	time*Out/in MPA	7	-330.91	676.01	0.32	0.34
	3	time+Out/in MPA	6	-332.23	676.61	0.91	0.25
	4	Null	4	-338.95	685.97	10.27	0.00
	5	Out/in MPA	5	-338.45	687.01	11.31	0.00
Breeding success (540)	**1**	**time*Out/in MPA**	**7**	**-363.95**	**742.11**	**0.00**	**0.90**
	2	Null	4	-370.22	748.52	6.40	0.04
	3	Out/in MPA	5	-369.39	748.89	6.78	0.03
	4	time	5	-369.99	750.09	7.98	0.02
	5	time+Out/in MPA	6	-369.16	750.48	8.37	0.01
N eggs laid - threshold (541)	**1**	**Null**	**3**	**-815.09**	**1636.22**	**0.00**	**0.45**
	2	Threshold	4	-814.76	1637.59	1.37	0.22
	3	Out/in MPA	4	-815.04	1638.15	1.94	0.17
	4	Threshold+Out/in MPA	5	-814.71	1639.52	3.31	0.09
	5	Threshold*Out/in MPA	6	-813.82	1639.80	3.59	0.07
N eggs hatched - threshold (730)	**1**	**Threshold*Out/in MPA**	**6**	**-1185.80**	**2383.72**	**0.00**	**0.33**
	2	**Null**	**3**	**-1189.03**	**2384.09**	**0.37**	**0.28**
	3	Out/in MPA	4	-1188.37	2384.81	1.08	0.19
	4	Threshold	4	-1188.87	2385.79	2.07	0.12

	5	Threshold+Out/in MPA	5	-1188.24	2386.57	2.85	0.08
N chicks fledged - threshold (744)	**1**	**Threshold*Out/in MPA**	**6**	**-1057.48**	**2127.06**	**0.00**	**0.99**
	2	Threshold	4	-1064.45	2136.95	9.88	0.01
	3	Threshold+Out/in MPA	5	-1063.49	2137.05	9.99	0.01
	4	Null	3	-1068.37	2142.77	15.71	0.00
	5	Out/in MPA	4	-1067.52	2143.09	16.02	0.00
Hatching success - threshold (538)	**1**	**Threshold*Out/in MPA**	**6**	**-293.58**	**599.31**	**0.00**	**0.94**
	2	Threshold	4	-299.13	606.34	7.02	0.03
	3	Threshold+Out/in MPA	5	-298.75	607.60	8.29	0.01
	4	Null	3	-301.27	608.59	9.28	0.01
	5	Out/in MPA	4	-300.86	609.80	10.49	0.00
Fledging success - threshold (576)	**1**	**Threshold*Out/in MPA**	**6**	**-328.36**	**668.86**	**0.00**	**0.67**
	2	Threshold	4	-331.58	671.23	2.37	0.20
	3	Threshold+Out/in MPA	5	-331.05	672.21	3.35	0.13
	4	Null	3	-345.83	697.71	28.85	0.00
	5	Out/in MPA	4	-345.50	699.07	30.21	0.00
Breeding success - threshold (540)	**1**	**Threshold*Out/in MPA**	**6**	**-361.24**	**734.63**	**0.00**	**0.99**
	2	Null	3	-370.22	746.49	11.85	0.00
	3	Out/in MPA	4	-369.39	746.86	12.22	0.00
	4	Threshold	4	-370.08	748.24	13.61	0.00
	5	Threshold+Out/in MPA	5	-369.24	748.60	13.97	0.00

b) Estimated coefficients of variables influencing the reproductive parameters in Corsican ospreys, in the selected models.

Model Set	N_model set	Variables	B	0.95 confidence intervals	
N eggs laid	1	Intercept	1.046	0.99	1.09
N eggs hatched	1	Intercept	0.497	0.207	0.787
		time	0.005	-0.0044	0.0156
		Out/in MPA (IN)	0.264	-0.088	0.616
		time*Out/in MPA (IN)	-0.015	-0.151	-0.0014
	2	Intercept	0.617	0.475	0.751
N chicks fledged	1	Intercept	0.4502	-0.0626	0.9409
		time	-0.0115	-0.0317	0.0089
		Out/in MPA (IN)	0.474	0.0625	0.8828
		time*Out/in MPA (IN)	-0.030	-0.0475	-0.0144
Hatching success	1	Intercept	-0.251	-2.2174	1.4739
		time	0.034	-0.0339	0.1113
		Out/in MPA (IN)	4.095	1.859	6.7324
		time*Out/in MPA (IN)	-0.153	-0.2403	-0.077
Fledging success	1	Intercept	2.823	1.838	3.948
		time	-0.083	-0.127	-0.045
Breeding success	1	Intercept	-0.579	-1.382	0.171
		time	0.024	-0.001	0.052

		Out/in MPA (IN)	2.195	0.520	4.024
		time*Out/in MPA (IN)	-0.092	-0.153	-0.035
N eggs laid – threshold	1	Intercept	1.046	0.996	1.096
N eggs hatched – threshold	1	Intercept	0.677	0.572	0.774
		Threshold (before)	-0.132	-0.322	0.0569
		Out/in MPA (IN)	-0.177	-0.362	-0.0007
		Threshold (before)*Out/in MPA (IN)	0.345	0.0392	0.647
	2	Intercept	0.630	0.541	0.711
N chicks fledged – threshold	1	Intercept	0.154	-0.029	0.326
		Threshold (before)	0.233	-0.045	0.518
		Out/in MPA (IN)	-0.395	-0.684	-0.120
		Threshold (before)*Out/in MPA (IN)	0.618	0.269	0.969
Hatching success – threshold	1	Intercept	1.0999	0.634	1.579
		Threshold (before)	-1.549	-2.622	-0.538
		Out/in MPA (IN)	-0.499	-1.071	0.049
		Threshold (before)*Out/in MPA (IN)	3.377	1.207	6.547
Fledging success – threshold	1	Intercept	0.509	0.129	0.890
		Threshold (before)	1.707	0.887	2.629
		Out/in MPA (IN)	-0.523	-1.168	0.101
		Threshold (before)*Out/in MPA (IN)	2.149	0.295	5.135
Breeding success – threshold	1	Intercept	0.175	-0.134	0.472
		Threshold (before)	-0.868	-1.695	-0.090
		Out/in MPA (IN)	-0.657	-1.250	-0.066
		Threshold (before)*Out/in MPA (IN)	3.723	1.738	6.770

c) Results of model selection of GLMM on the effects of boat traffic on behavioural parameters of Corsican breeding ospreys. Selected models are shown in bold.

Response variable	Model	Variables retained	K	logLik	AICc	ΔAICc	Weight
N of prey items brought to the nest per hour (41)	**1**	**Traffic**	**6**	**43.48**	**-72.48**	**0.00**	**0.85**
	2	Null	5	40.34	-68.97	3.51	0.15
N of disturbing events (41)	**1**	**Traffic**	**6**	**-5.28**	**25.03**	**0.00**	**0.9**
	2	Null	5	-8.86	29.44	4.41	0.1
N of flight off events (41)	1	**Traffic**	6	**-52.64**	**119.75**	**0.00**	**0.56**
	2	**Null**	5	**-54.27**	**120.26**	**0.52**	**0.44**
Time female alarming (41)	1	**Traffic**	6	**-55.94**	**126.35**	**0.00**	**0.71**
	2	**Null**	5	**-58.23**	**128.17**	**1.82**	**0.29**

d) Estimated coefficients of variables influencing the behavioural parameters of Corsican breeding ospreys, in the selected models.

Model Set	N_model set	Variables	B	0.95 confidence intervals	
N of prey items brought to the nest per hour	1	Intercept	0.162	0.1134	0.2158
		Traffic (high)	-0.092	-0.1694	-0.0232
N of disturbing events	1	Intercept	-0.243	-0.627	0.1081
		Traffic (high)	0.216	0.066	0.371
N of flight off events	1	Intercept	0.435	-0.101	0.974
		Traffic (high)	0.729	-0.071	1.489
	2	Intercept	0.774	0.317	1.248
Time female alarming	1	Intercept	-0.656	-1.749	0.399
		Traffic (high)	0.493	0.047	0.925
	2	Intercept	0.386	-0.286	0.988