Animal Conservation

Volume 21 | December 2018 | Number 6

The rapid publication journal for quantitative studies in conservation

FEATURE PAPER: Integrative long-term study reveals eco-tourism impacts on a flagship species at a UNESCO site

ZSL
LET'S WORK FOR WILDLIFE

Volume 21 | Number 6 | December 2018 | Pages 445–534

Animal Conservation

Front cover:
Tourist boat approaching an osprey nest, located at the top of a rocky pinacle, in the UNESCO world heritage site Scandola National Nature Reserve, Corsica, June 2014
Photo: Olivier Duriez

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Animal Conservation

Animal Conservation. Print ISSN 1367-9430

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

F. Monti[1,2,3], O. Duriez[1], J.-M. Dominici[4], A. Sforzi[5], A. Robert[1], L. Fusani[2,6] & D. Grémillet[1,7]

1 CEFE UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, Montpellier Cedex 5, France
2 Department of Life Sciences and Biotechnology, University of Ferrara, Ferrara, Italy
3 Department of Physical Sciences, Earth and Environment, University of Siena, Siena, Italy
4 Réserve Naturelle Scandola, Parc Naturel Régional de Corse, Galeria, France
5 Maremma Natural History Museum, Grosseto, Italy
6 Department of Cognitive Biology, University of Vienna, and Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria
7 FitzPatrick Institute, DST/NRF Centre of Excellence at the University of Cape Town, Rondebosch, South Africa

Keywords
Corticosterone; Osprey; Mediterranean; MPA; GPS tracking; disturbance; ecotourism; breeding failure.

Correspondence
Flavio Monti, Department of Physical Sciences, Earth and Environment, University of Siena, Strada Laterina, 8, 53100 Siena, Italy.
Tel: +390564488570;
Email: flaviomonti00@gmail.com

Editor: Gurutzeta Guillera-Arroita
Associate Editor: Cristian Bonacic

Received 14 November 2016; accepted 22 January 2018

doi:10.1111/acv.12407

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, epipelagic 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

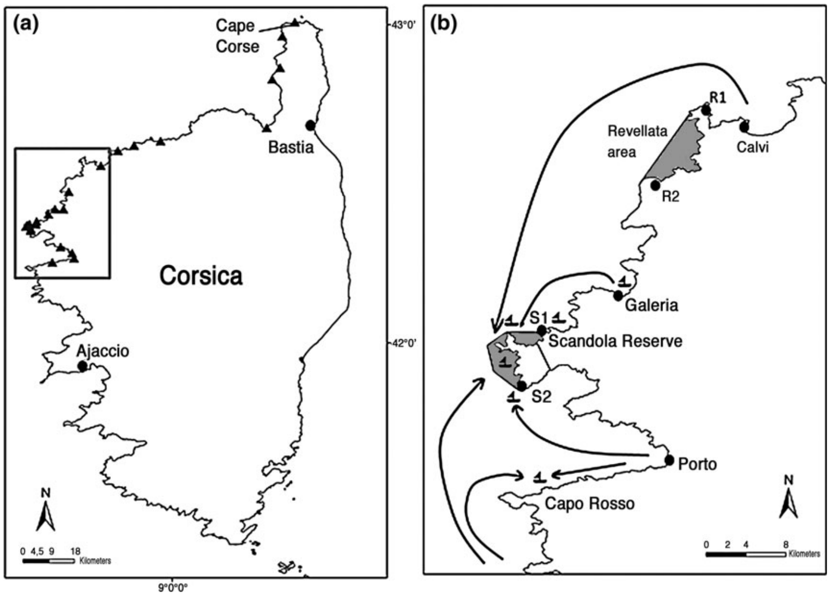

Figure 1 (a) Location of osprey nests in Corsica, where the 24 transects of fish sampling have been performed (see Appendix S1: Fig. 1c–d); (b) zoom on the Scandola marine protected area and the Revellata areas (coloured in grey); for each area land-based vantage-points are reported as: S1, S2, R1, R2; 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 ≤ 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 ± 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

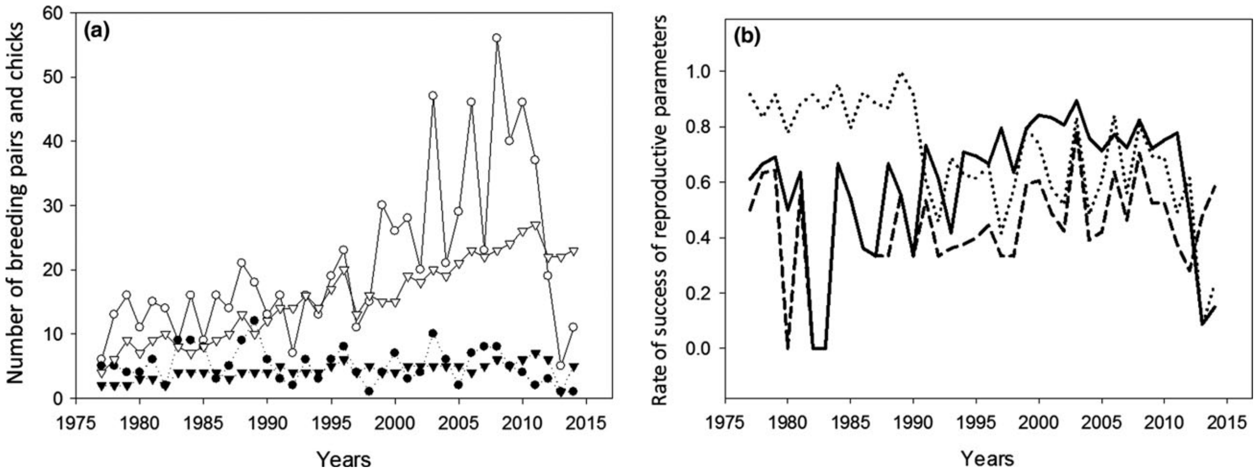

Figure 2 Historical trend of the Corsican osprey population in 1977–2014: (a) number of breeding pairs and chicks fledged outside of the marine-protected area (MPA) (white triangles and dots, respectively) and inside the MPA (black triangles and dots, respectively); (b) hatching success (dashed line), 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

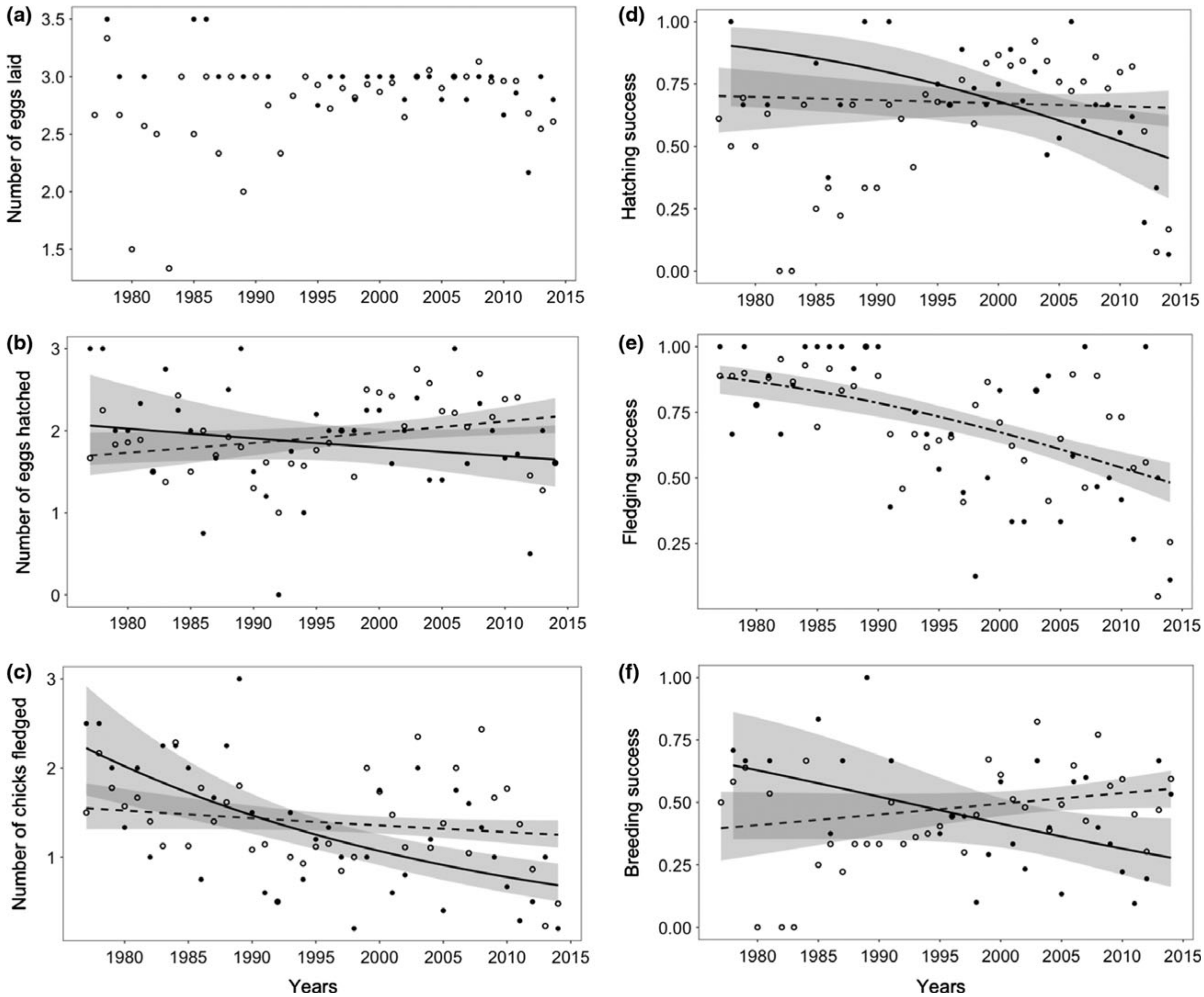

Figure 3 Historical trend in Corsican osprey breeding parameters inside the Scandola marine-protected area (MPA) (black dots and solid line) and outside MPA (white dots and dotted line): (a) number of eggs laid; (b) number of eggs hatched; (c) number of chicks fledged; (d) hatching success; (e) fledging 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

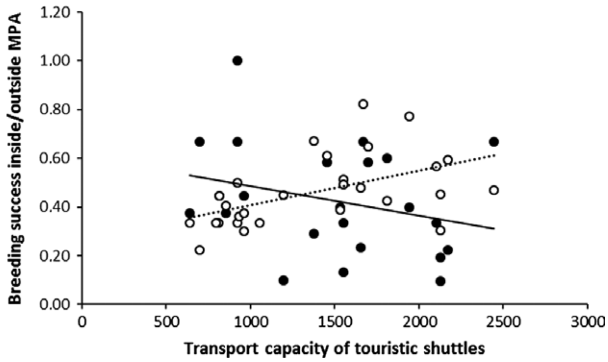

Figure 4 Correlations between breeding success inside the marine-protected area (MPA) (black dots and solid line; Spearman's rank correlation, rho = −0.289, $P = 0.181$) and outside the MPA (white dots and dotted line; rho = 0.557, $P = 0.002$) and transport capacity of touristic shuttles (calculated 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).

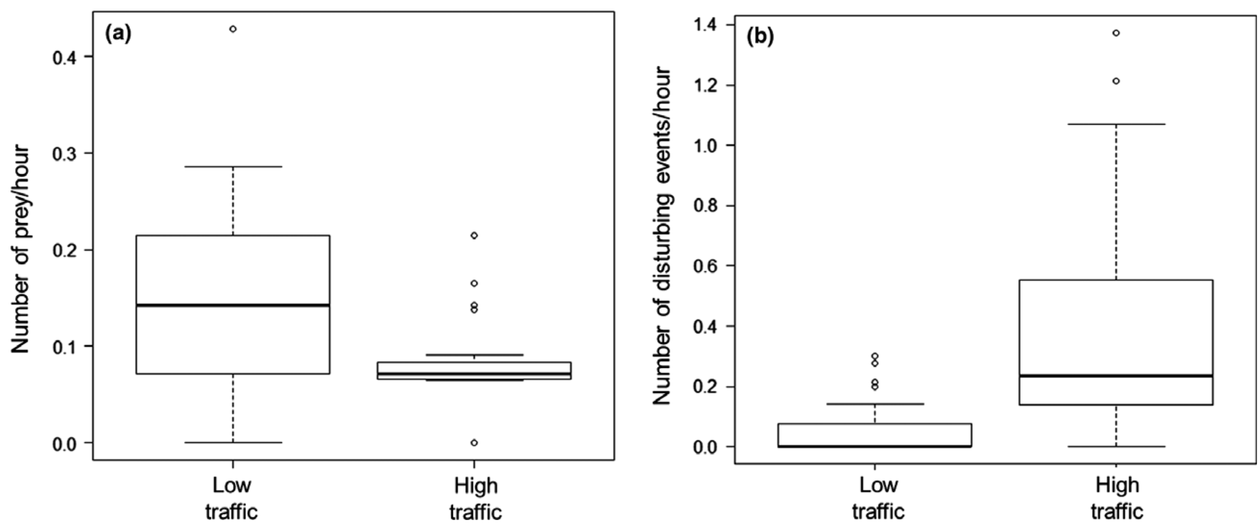

Figure 5 (a) Number of prey items brought to the nest per hour by male ospreys and (b) disturbing events per hour in 'low-traffic' and 'high-traffic' areas in Corsica.

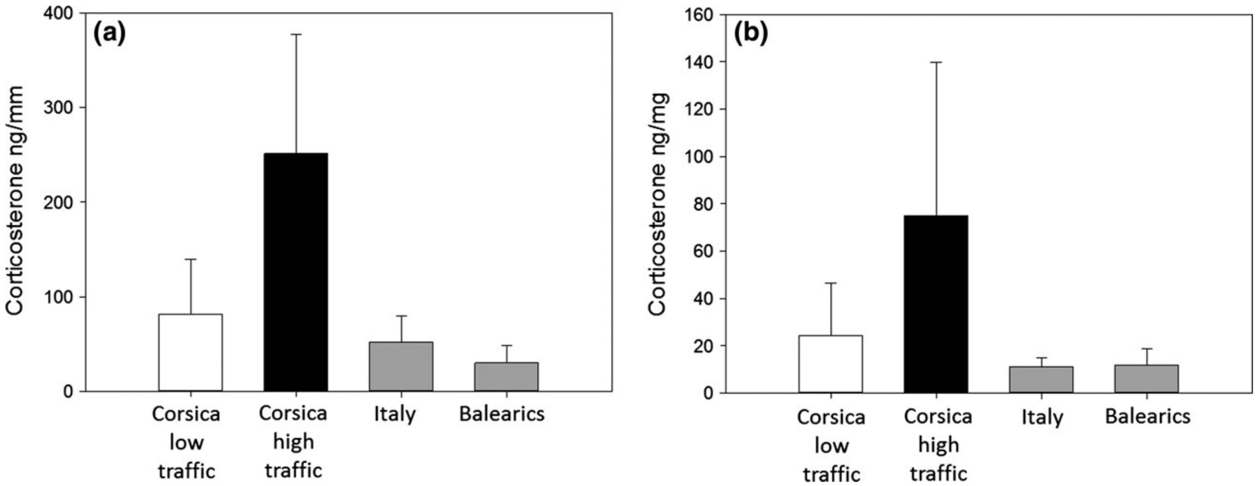

Figure 6 Mean values of (a) corticosterone temporal expression (ng/mm) and (b) its concentration (ng/mg) for each locality. Corsica has been split in low- and high-traffic areas (respectively white and black bars); other control sites (Italy and Balearics) in grey bars.

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

We thank the former and actual presidents of the Parc Naturel Régional de Corse, Jean-Luc Chiappini and Jacques Costa, and the director Philippe Porruncini, staff of Scandola MPA (J. Albertini, V. Le Normand, J. Tavernier, S.A. Rossi and F. Paolini), A. Camoin, M. Delpuech, C. Chancellier, G. Valesi, M. D'Addario, M. Amiguet, I. Fraccaroli, A. Ferretti, J. Fluhr and F. Delfour for their assistance during fieldwork. The equipment to attach camera to kayak was built by the Plateforme Terrains d'Experiences of CEFE. We thank Rafel Triay Bagur who provided feather samples from Balearic Islands. We are grateful to Virginie Canoine for the help with corticosterone extractions and to Francesco Ferretti and Niccolò Fattorini for their help with statistical tests. This study was funded by the Foundation Prince Albert II de Monaco and the Associazione italiana della Fondation Prince Albert II de Monaco ONLUS, the Parc Naturel Régional de Corse, Maremma Regional Park and Conservatoire du Littoral (through the Mediterranean Small Islands Initiative PIM). F. Monti was supported by the Maremma Regional Park (Italy) and the Università Italo Francese/Université Franco Italienne (UIF/UFI).

References

Aburto-Oropeza, O., Erisman, B., Galland, G.R., Mascareñas-Osorio, I., Sala, E. & Ezcurra, E. (2011). Large recovery of fish biomass in a no-take marine reserve. *PLoS ONE* **6**, e23601.

Badalamenti, F., Ramos, A.A., Voultsiadou, E., Sánchez Lizaso, J.L., D'Anna, G., Pipitone, C., Mas, J., Fernandez, J.R., Whitmarsh, D. & Riggio, S. (2000). Cultural and socio-economic impacts of Mediterranean marine protected areas. *Environ. Conserv.* **27**, 110–125.

Bartoń, K. (2012). *MuMIn: multi-model inference*. Vienna: R Foundation for Statistical Computing.

Bolduc, F. & Guillemette, M. (2003). Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. *Biol. Cons.* **110**, 77–83.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135.

Bortolotti, G.R., Marchant, T.A., Blas, J. & German, T. (2008). Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Funct. Ecol.* **22**, 494–500.

Bortolotti, G.R., Marchant, T., Blas, J. & Cabezas, S. (2009). Tracking stress: localisation, deposition and stability of corticosterone in feathers. *J. Exp. Biol.* **212**, 1477–1482.

Bracciali, C., Campobello, D., Giacoma, C. & Sarà, G. (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *PLoS ONE* **7**, e40582.

Bretagnolle, V. & Thibault, J.-C. (1993). Communicative behavior in breeding ospreys (*Pandion haliaetus*): description and relationship of signals to life history. *Auk* **110**, 736–751.

Bretagnolle, V., Mougeot, F. & Thibault, J.-C. (2008). Density dependence in a recovering osprey population: demographic and behavioural processes. *J. Anim. Ecol.* **77**, 998–1007.

Buckley, R.C. (2004). Impacts of ecotourism on birds. In *Environmental impacts of ecotourism*: 187–209. Buckley, R. (Ed). Wallingford: CAB International.

Buckley, R.C., Morrison, C. & Castley, J.G. (2016). Net effects of ecotourism on threatened species survival. *PLoS ONE* **11**, e0147988. https://doi.org/10.1371/journal.pone.0147988.

Cabeza, M., Arponen, A. & Van Teeffelen, A. (2008). Top predators: hot or not? A call for systematic assessment of biodiversity surrogates. *J. Appl. Ecol.* **45**, 976–980.

Crawley, M.J. (2007). *The R book*. Chichester: John Wiley and Sons Ltd.

Crooks, K.R. & Sanjayan, M.A. (2006). *Connectivity conservation*. Cambridge, New York: Cambridge University Press. Available from http://site.ebrary.com/id/10202782 (accessed November 19, 2014).

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M. & Thomson, R.J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220.

Francour, P. (1994). Pluriannual analysis of the reserve effect on ichthyofauna in the scandola natural reserve (Corsica, northwestern mediterranean). *Oceanol. Acta* **17**, 309–317.

Francour, P. & Thibault, J.-C. (1996). The diet of breeding Osprey *Pandion haliaetus* on Corsica: exploitation of a coastal marine environment. *Bird Study* **43**, 129–133.

Francour, P., Harmelin, J.-G., Pollard, D. & Sartoretto, S. (2001). A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. *Aquat. Conserv.* **11**, 155–188.

Fraser, D.J. & Bernatchez, L. (2001). Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* **10**, 2741–2752.

Friedman, M. (1937). The use of ranks to avoid the assumption of normality implicit in the analysis of variance. *J. Am. Stat. Assoc.* **32**, 675–701.

González, L.M., Arroyo, B.E., Margalida, A., Sánchez, R. & Oria, J. (2006). Effect of human activities on the behaviour of breeding Spanish imperial eagles (*Aquila adalberti*): management implications for the conservation of a threatened species. *Anim. Conserv.* **9**, 85–93.

Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M. & Sala, E. (2014). Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. *PLoS ONE* **9**, e91841. https://doi.org/10.1371/journal.pone.0091841.

Hausmann, A., Slotow, R., Fraser, I. & Di Minin, E. (2017). Ecotourism marketing alternative to charismatic megafauna can also support biodiversity conservation. *Anim. Conserv.* **20**, 91–100. https://doi.org/10.1111/acv.12292.

Hood, G.A. & Parker, K.L. (2001). Impact of human activities on grizzly bear habitat in Jasper National Park. *Wildl. Soc. Bull.* **29**, 624–638.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B. & Hornocker, M.G. (2002). Effects of roads and human disturbance on Amur tigers. *Conserv. Biol.* **16**, 97–108.

Le Diréach, L., Bonhomme, P., Boudouresque, C.F. & Cadiou, G. (2010). Fishing effort and catches in the marine protected area of Scandola and adjancent areas (Corsica, Mediterranean). *Rapp. Comm. Int'l Mer. Mediterr.* **39**, 770.

Le Saout, S., Hoffman, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T. & Rodrigues, A.S.L. (2014). Protected areas and effective biodiversity conservation. *Science* **342**, 803–805. https://doi.org/10.1126/science.1239268.

Leenhardt, P., Cazalet, B., Salvat, B., Claudet, J. & Feral, F. (2013). The rise of large-scale marine protected areas: conservation or geopolitics? *Ocean Coast. Manag.* **85**, 112–118.

Lloret, J., Zaragoza, N., Caballero, D. & Riera, V. (2008). Impacts of recreational boating on the marine environment of Cap de Creus (Mediterranean Sea). *Ocean Coast. Manag.* **51**, 749–754.

Love, O.P., Bird, D.M. & Shutt, L.J. (2003). Corticosterone levels during post-natal development in captive American kestrels (*Falco sparverius*). *Gen. Comp. Endocrinol.* **130**, 135–141.

Lubchenco, J. & Grorud-Colvert, K. (2015). Making waves: the science and politics of ocean protection. *Science* **350**, 382–383.

Martinez-Abrain, A., Oro, D., Jimenez, J., Stewart, G. & Pullin, A. (2010). A systematic review of the effects of recreational activities on nesting birds of prey. *Basic Appl. Ecol.* **11**, 312–319.

McClung, M.R., Seddon, P.J., Massaro, M. & Setiawan, A.N. (2004). Nature-based tourism impacts on yellow-eyed penguins Megadyptes antipodes: does unregulated visitor access affect fledging weight and juvenile survival? *Biol. Cons.* **119**, 279–285.

Monti, F. (2012). *The Osprey, Pandion haliaetus. State of knowledge and conservation of the breeding population of the Mediterranean basin*. Initiative PIM.

Monti, F., Nibani, H., Dominici, J.M., Rguibi Idrissi, H., Thévenet, M., Beaubrun, P.C. & Duriez, O. (2013). The vulnerable Osprey breeding population of the Al Hoceima National Park, Morocco: present status and threats. *Ostrich* **84**, 199–204.

Monti, F., Dominici, J.M., Choquet, R., Duriez, O., Sammuri, G. & Sforzi, A. (2014). The Osprey reintroduction in Central Italy: dispersal, survival and first breeding data. *Bird Study* **61**, 465–473.

Monti, F., Duriez, O., Arnal, V., Dominici, J.M., Sforzi, A., Fusani, L., Grémillet, D. & Montgelard, C. (2015). Being cosmopolitan: evolutionary history and phylogeography of a specialized raptor, the Osprey *Pandion haliaetus*. *BMC Evol. Biol.* **15**, 225.

Morvan, G. (2010). *Suivi de la fréquentation touristique et récréative du littoral de la Réserve Naturelle de Scandola par les engins et bateaux de plaisance et les vedettes à passagers de l'été 2010*. Ajaccio: Parc naturel régional de corse.

Müllner, A., Eduard Linsenmair, K. & Wikelski, M. (2004). Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biol. Cons.* **118**, 549–558.

Pauli, B.P., Spaul, R.J. & Heath, J.A. (2017). Forecasting disturbance effects on wildlife: tolerance does not mitigate effects of increased recreation on wildlands. *Anim. Conserv.* **20**, 251–260. https://doi.org/10.1111/acv.12308.

Péron, C., Grémillet, D., Prudor, A., Pettex, E., Saraux, C., Soriano-Redondo, A., Authier, M. & Fort, J. (2013). Importance of coastal Marine Protected Areas for the conservation of pelagic seabirds: the case of Vulnerable yelkouan shearwaters in the Mediterranean Sea. *Biol. Cons.* **168**, 210–221.

Pichegru, L., Gremillet, D., Crawford, R.J.M. & Ryan, P.G. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biol. Let.* **6**, 498–501.

Poole, A.F. (1989). *Ospreys: a natural and unnatural history*. Cambridge: Cambridge University Press.

Richards, S.A. (2008). Dealing with overdispersed count data in applied ecology. *J. Appl. Ecol.* **45**, 218–227.

Richards, S.A., Whittingham, M.J. & Stephens, P. (2011). Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behav. Ecol. Sociobiol.* **65**, 77–89.

Richez, G. and Richez Battesti, J. (2007). *Patrimoine naturel et développement économique des territoires. La Réserve naturelle de Scandola (Corse) et le transport maritime côtier de loisir*. Rapport au Parc naturel régional de la Corse.

Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C. & Dayton, P. (2002). A general model for designing networks of marine reserves. *Science* **298**, 1991–1993. https://doi.org/10.1126/science.1075284.
Selig, E.R. & Bruno, J.F. (2010). A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS ONE* **5**, e9278.
Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *J. Appl. Ecol.* **43**, 1049–1055.
Star, S.L. & Griesemer, J.R. (1989). Institutional ecology, 'translations' and boundary objects: amateurs and professionals in Berkeley's museum of vertebrate zoology, 1907–39. *Soc. Stud. Sci.* **19**, 387–420.
Steven, R., Pickering, C. & Castley, J.G. (2011). A review of the impacts of nature based recreation on birds. *J. Environ. Manage.* **92**, 2287–2294.
Steven, R., Castley, J.G. & Buckley, R.C. (2013). Tourism revenue as a conservation tool for threatened birds in protected areas. *PLoS ONE* **8**, e62598.
Tavernier, J. (2010). *Plan de gestion de la réserve naturelle de Scandola 2010–2020*. Parc naturel régional de la Corse.
Thibault, J.C., Bretagnolle, V. & Dominici, J.M. (2001). *Le Balbuzard pêcheur en Corse: du martyre au symbole de la protection de la nature*. Ajaccio: Alain Piazzola.
Thiel, D., Jenni-Eiermann, S., Palme, R. & Jenni, L. (2011). Winter tourism increases stress hormone levels in the Capercaillie *Tetrao urogallus*. *The Ibis* **153**, 122–133.
Thurstan, R.H., Hawkins, J.P., Neves, L. & Roberts, C.M. (2012). Are marine reserves and non-consumptive activities compatible? A global analysis of marine reserve regulations. *Mar. Policy* **36**, 1096–1104.
Velando, A. & Munilla, I. (2011). Disturbance to a foraging seabird by sea-based tourism: implications for reserve management in marine protected areas. *Biol. Cons.* **144**, 1167–1174.
Zuur, A.F., Ieno, E.N., Walker, N.J., Savellev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

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.