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Outdoor recreation alters terrestrial vertebrate scavenger assemblage and carrion removal in a protected Mediterranean wetland

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Abstract

Outdoor recreation has increased in recent decades, with an intensification after the COVID-19 lockdown. Previous studies have shown that disturbances from this activity may affect species behaviour and fitness, but its effect on ecological processes has been overlooked. Here, we test the impact of outdoor recreation on terrestrial vertebrate scavenger assemblage and scavenging patterns in El Hondo Natural Park, a Mediterranean wetland located in south-eastern Spain. We placed 185 carcasses monitored with camera traps between February 2020 and May 2021 in two areas: ‘public access area’, where visitors can freely access and carry out outdoor recreation, and ‘restricted area’, where visitors are not allowed. Our results showed that outdoor recreation altered the scavenger assemblage composition, especially affecting large species such as raptors. Non-native species scavenged almost four times more often on carcasses in public access areas than in the restricted areas, showing that human activities promote the presence of non-native species. Furthermore, vertebrates completely consumed 68.2% of the carcasses in the restricted area, decreasing to 46.7% in the public access area. In the restricted area, consumption time was shorter (111.8 vs. 157.5 h) and consumed biomass by vertebrate scavengers was larger (73.9 vs. 52.2%) than in public access area, evidencing that outdoor recreation also affects scavenging processes. Our study shows that outdoor recreation profoundly alters not only the scavenger assemblage but also key ecological processes such as carrion removal. This highlights the urgency of regulating tourism and maintaining restricted areas to preserve biodiversity and ecological processes, especially in highly anthropized landscapes.

Introduction

Protected areas (PAs) have traditionally been created to preserve biodiversity and ecosystems worldwide (Geldmann *et al.*, 2013; Gray *et al.*, 2016). However, since the 1980s, PAs are managed with a dual objective; on the one hand, they aim to preserve biodiversity, but, on the other hand, they are also designed to improve the development of local human communities and human well-being in general (Naughton-Treves, Holland, & Brandon, 2005). This duality has generated a new framework for PAs, where public access is allowed and outdoor recreation is encouraged (McNeely, 1994), triggering a debate about what should be PAs' priority. Globally, PAs receive about 8 billion visitors per year (Balmford *et al.*, 2015) and these are expected to increase (Bowker *et al.*, 2012). In addition, after the pandemic and in the wake of the COVID-19 lockdown, there has been a burst in the number of visitors at PAs to mitigate impacts associated with isolation measures and mental stress, looking for outdoor green areas, but further increasing pressure on ecosystems (Ma *et al.*, 2021; Primack & Terry, 2021).

Contact with nature is known to have many benefits for human health (Frumkin, 2001; McCurdy *et al.*, 2010), and can help build support for conservation (Zaradic, Pergams, & Kareiva, 2009), as well as being an economic driver for human communities surrounding PAs (Stem *et al.*, 2003). Nevertheless, outdoor recreation is not always compatible with nature conservation, and rapid growth coupled with poor practice may threaten PAs worldwide (Schulze *et al.*, 2018), raising great concern among scientists and environmentalists. A growing number of studies are showing that outdoor recreation can have adverse effects on wildlife (Larson *et al.*, 2016) such as altering habitat use (Rösner *et al.*, 2014), decreasing species survival and reproduction (Müllner, Eduard Linsenmair, & Wikelski, 2004; Iverson *et al*., 2006), producing physiological stress (Arlettaz *et al*., 2007), increasing surveillance (Mainini, Neuhaus, & Ingold, 1993), introducing non-native species (Reed & Merenlender, 2008), decreasing density (Thompson, 2015), richness and abundance of species (Larson *et al*., 2019), and altering community composition (Kangas *et al*., 2010), leading to the extirpation of otherwise suitable habitats (Steven & Castley, 2013). By contrast, the effect on the functioning of ecosystems and the ecological functions the species perform (e.g. seed dispersal, pollination, nutrient cycling, etc.) has been overlooked (Weiss, Brummer, & Pufal, 2016).

Scavengers play a key role in ecosystems, which, through carrion consumption, perform ecosystem functions and services such as food web maintenance and stabilization (Wilson & Wolkovich, 2011), disease and pest control (Markandya *et al*., 2008), rapid and effective nutrient recirculation (Wilson & Wolkovich, 2011), indirect greenhouse emissions regulation (Morales-Reyes *et al*., 2015) and cultural inspiration and recreational activities (García-Jiménez *et al*., 2022). Outdoor recreation is known to affect some scavengers, decreasing reproductive success in several vulture species (Arroyo & Razin, 2006; Zuberogoitia *et al*., 2008) and changing the behaviour and flight distance of raptors, crows and gulls (Skagen, Knight, & Orians, 1991; Stalmaster & Kaiser, 1998; Perona, Urios, & López-López, 2019). Nevertheless, how human recreation affects carrion consumption patterns and removal has not been assessed yet.

Our objective is to assess how outdoor recreation affects scavenger assemblage composition and carrion consumption patterns in a protected wetland from the Mediterranean basin. Wetlands support a great amount of global biodiversity and contribute disproportionately to the provision of ecosystem services worldwide, yet they are one of the most threatened habitats on Earth (Balian *et al*., 2008; Davidson *et al*., 2019). Suitable protection and conservation of these habitats is key to maintaining biodiversity, especially in highly transformed areas such as the Mediterranean basin, where *C*. 50% of wetland areas have been lost in the 20th century (Perennou *et al*., 2012). Besides habitat transformation, wetlands suffer greater pressure from tourism and outdoor recreation than other natural areas, as they frequently overlap with touristic areas close to the coast (Cardoni, Favero, & Isacch, 2008). Therefore, the effects of outdoor recreation on ecosystem functioning are expected to be more intense in these areas.

This study was done in a protected wetland in south-eastern Spain intensively visited by tourists. This Natural Park is divided into two areas according to their use: ‘public access area’, where visitors can freely access and carry out outdoor recreation (i.e. cycling, running, hiking, birdwatching, picnicking or dog walking) and ‘restricted area’ where visitors are not allowed. Moreover, the number of visitors has increased at an alarming rate after the COVID-19 lockdown. In 2021, visitors increased by 24% compared to 2019, the year with the highest number of visitors ever (34 806 visitors vs. 28 118 visitors respectively; data provided by the administration of the Natural Park). Thus, we studied the terrestrial vertebrate scavenger assemblage and carrion consumption patterns in the two defined areas according to visitor access. We hypothesized that the composition of the scavenger assemblage will be different in the public access and restricted areas. We predict that larger scavenger species such as raptors (Skagen, Knight, & Orians, 1991) and some carnivorous mammalian species (Reed & Merenlender, 2008) will be the most affected by human use, as they are more sensitive to human activities (Cooke, 1980). We also hypothesized that human visitation will have negative effects on carrion consumption and removal, increasing the time that carrion is prevalent in the environment. Finally, we compared carrion consumption of non-native species between public access and restricted areas. Habitat disturbance and human use of natural areas can facilitate the introduction of non-native species (Gilby *et al*., 2022), so we expected non-native species to be more abundant in the public access area.

Materials and methods

Study area

The study was conducted in El Hondo Natural Park (38°11′16″N, 0°47′28″O), south-eastern Spain. El Hondo is a semi-natural mesohaline coastal wetland with an extension of 2387 ha, composed of two large ponds used for crop irrigation and about 20 smaller ponds used for conservation, sport fishing or as waterfowl hunting grounds. Our survey was carried out only in the ponds that are used for crop irrigation and conservation, since the hunting grounds and sport fishing ponds are privately owned. The Natural Park is composed of different ecosystems: the reedbed is the predominant ecosystem occupying most of the surface, especially surrounding the ponds. The marsh, which is composed of aquatic species such as *Schoenoplectus litoralis* and *Bolboschoenus maritimus*. The saltmarshes, which are areas that remain permanently dry with species adapted to high soil salinity such as *Salicornia* spp., *Halocnemum strobilaceum*, *Limonium* spp. and *Tamarix* spp. Climate is dry thermo-Mediterranean with an annual rainfall of <300 mm and an average annual temperature of 18°C.

El Hondo is a Ramsar site protected by the European Habitat and Bird Directive (Directive 92/43/CEE), included in the NATURA-2000 network of the European Union. This wetland is considered of global importance because it hosts an important wintering and breeding waterfowl community. It is also home to important populations of raptors, gulls and mesocarnivores as the red fox *Vulpes*, the stone marten *Martes foina* or the common genet *Genetta genetta*, which are potential scavengers.

Study design

Two areas were designated within the El Hondo Natural Park for carcass placement: the restricted area and the public access area. The restricted area cannot be accessed by visitors to the Natural Park and is used for species conservation, and as a water reservoir for irrigation of the agricultural fields in the region. The public access area is destined for the conservation of the species and ecosystems at the Natural Park, but the visitors of the park can freely access it. In the public access area, there are trails, birdwatching and picnic zones, which are used for cycling, running, hiking, birdwatching, picnics or dog walking among other activities. The two areas have the same type of ecosystem, are adjacent and not fenced, so animals can freely move among them.

Between February 2020 and May 2021, we placed 185 carcasses in the Natural Park monitored with camera traps (model: Browning Strike Force pro HD), 110 in the restricted area (1278 ha) and 75 in the public access area (270 ha). One of the carcasses was excluded from the analysis because it was submerged in the water when the pond flooded. Carcasses were from animals of different taxa that can be found at the Natural Park (n = 36 species), such as fish (i.e. common carp *Cyprinus carpio*; 200–3975 g; n = 86), terrestrial birds (i.e. turtledoves, quails, cuckoos and passerines; 10–202 g; n = 36), mammals (rodents, shrews, hares and rabbits; 8–2254 g; n = 33) and waterbirds (waders and ducks: 106–3450 g; n = 30). Carcass details can be found in the original database (Orihuela-Torres, Sebastián-González, & Perez-García, 2022). Carcasses of terrestrial wildlife were collected from roadkills in the surroundings of the Natural Park and from the regional wildlife rescue centre, while fish were caught by the Natural Park staff in the park ponds as part of the programme for the elimination of invasive species. Waterbirds were placed near the ponds, fish on the shore of the ponds, and mammals and terrestrial birds throughout the Natural Park mimicking natural mortality. Carcasses were disposed all year round to account for possible seasonal differences in the scavenging patterns (Orihuela-Torres, Pérez-García, Sánchez-Zapata, Botella, & Sebastián-González, 2022), and at least 200 m apart. Some carcasses were placed at a closer distance (<25 m apart), but with at least 1 month of difference, to avoid scavengers getting used to the supply of carrion (Turner, Conner, & Beasley, 2020). Two cameras were placed at each carrion, one in photo mode and one in video mode, to confirm carrion consumption in case of doubt. Photo mode cameras were programmed to take three3 photos every 30 s, while the video mode cameras took a 20-s video every minute when motion was detected. Cameras were left for 15 days or until the carcass was completely consumed (except for the skeleton and skin or feathers). Carcasses were checked every 3 days at the latest to be monitored in detail.

Data analysis

Variables

We used the information from the cameras to calculate the following variables: (i) ‘richness’: number of species consuming the carcass; (ii) ‘abundance’: number of individuals consuming the carcass. This is the maximum number of individuals recorded consuming in a single photo or video. When they do not appear in the same photo or video, they may be differentiated by sex, age or marks (Sebastián-González *et al*., 2019); (iii) ‘detection time’: time it takes for the first scavenger to feed on the carcass since placement time; (iv) ‘consumption time’: time it takes for the carcass to be completely consumed (except skeleton) since placement time; (v) ‘consumed biomass’: percentage of biomass consumed (except skeleton) when the camera was removed. The percentages were estimated visually at 5% intervals. We calculated the total consumed biomass (vertebrates + invertebrates) and the vertebrate consumed biomass (the % of the carcass consumed by vertebrates). To determine the vertebrate consumption, we visited the carcasses every 3 days and noted the % biomass consumed in each visit. To differentiate between consumption by vertebrates and by invertebrates, we used visible marks in the carcass (e.g. bites, pecks or missing carcass parts are typical of vertebrates’ consumption) and information from the visualization of the videos and photos.

Statistical analysis

We fitted generalized linear models (GLMs) to test the differences in vertebrate scavenger species richness and abundance, as well as carrion consumption patterns between the type of Natural Park use (public access area vs. restricted area). ‘Richness’, ‘abundance’, ‘detection time’, ‘consumption time’ and ‘consumed biomass’ were the response variables, while ‘type of Natural Park use’ was the categorical predictor. We also included ‘carcass weight’ and ‘carcass type’ (i.e. fish, terrestrial bird, mammal or waterbird) as covariates in the models to control for the possible effect of these variables, as it is known from previous studies that the size and type of carcass are major factors in structuring the scavenger assemblage (Moleón *et al*., 2015; Olson, Beasley, & Rhodes, 2016). We run one model for each response variable with the predictor and the two covariates included in the same model. We used Poisson distribution for ‘richness’ and ‘abundance’, Gaussian distribution for ‘detection time’ and ‘consumption time’, and the binomial distribution for ‘consumed biomass’. ‘Detection time’ and ‘consumption time’ were log transformed to meet normality. To assess differences in assemblage composition (species identity and relative abundances) of vertebrate scavengers between Natural Park uses, we computed the permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) using the *vegan* (Oksanen *et al*., 2019) package in R (R Core Team, 2019).

Finally, we assessed the presence of non-native species by comparing the observed and expected-by-chance proportion of carcasses at which non-native species appear consuming carrion in each type of Natural Park use, using Chi-square tests.

Results

Overall scavenger assemblage and scavenging patterns

A total of 26 species (16 birds, nine mammals and one reptile) of vertebrate scavengers were recorded feeding on carrion (Table S1, Figures S1 and S2). The mammal species that consumed most carcasses were the brown rat *Rattus* *norvegicus*, the red fox and the wild boar *Sus scrofa*. The Eurasian magpie *Pica pica*, the common moorhen *Gallinula chloropus* and the Eurasian marsh-harrier *Circus aeroginosus* were the bird species most frequently found consuming carrion (Table S1).

In addition, we recorded three globally threatened species consuming carrion, the greater spotted eagle *Clanga clanga*, the red-knobbed coot *Fulica cristata* and the Iberian grey shrike *Lanius meridionalis*. Vertebrates were recorded in 78.1% (n = 143) of the carcasses, completely consuming 60.7% (n = 110; Table 1). Mammals appeared consuming in 48.1% (n = 88) of the carcasses, while birds occurred in 37.2% (n = 67).

Effect of public access

We found large differences in the composition of the vertebrate scavenger assemblages (PERMANOVA, F = 6.158, P < 0.001; Table S2) between the public access area and the restricted area. In the restricted area, we recorded 21 species of vertebrate scavengers (12 birds, eight mammals and one reptile) while in the public access area we recorded 15 species (11 birds and four mammals; Fig. 1; Table 1; Table S1). Our results support our first prediction, as larger species, such as the wild boar, the red fox and raptors, were practically absent in the public access area, whereas they were the species that consumed the most carrion in the restricted area. Unexpectedly however, this was not only the case with carnivores, but also the omnivore wild boar followed the same pattern. Some species such as the brown rat and the common moorhen were more abundant in the public access area, while gulls, the grey heron and the Eurasian magpie were equally present throughout the Natural Park (Fig. 1; Table S1). As expected, non-native species (i.e. brown rat, feral cat and dog) scavenged a significantly larger proportion of the carcasses in the public access (42.5%) than in the restricted area (11.8%) (χ^2 = 7.898, d.f. = 1, P = 0.004; Fig. 1), whereas we found the opposite pattern for native species (restricted area = 78.2% vs. public access area = 46.7%; χ^2 = 3.8552, d.f. = 1, P = 0.049; Fig. 1). We did not detect differences in species richness and mean abundance per carcass between the two types of Natural Park uses (Table 1).

There were also major differences in carrion consumption patterns (Tables 1 and 2; Table S3), in agreement with our second prediction. In the restricted area, vertebrates completely consumed 68.2% (n = 75) of the carcasses, whereas in the public access area they consumed 46.7% (n = 35). The proportion of consumed biomass by vertebrate scavengers was significantly larger in the restricted area (73.9%) than in the public access area (52.2%; Table 1; Table S3), and consumption times were significantly shorter (111.8 ± 121.6 h vs. 157.5 ± 135.4 h respectively), although no differences were found for the total biomass consumed including invertebrates (restricted = 85.1%, public access = 84.1%) nor for carcass detection times (Tables 1 and 2; Table S3). The weight and type of carcass also affected some response variables (Tables S3 and S4). In general, heavier and fish carcasses were consumed by more species and individuals. We also found that fish carcasses showed shorter detection and consumption times.

Discussion

Our findings show that outdoor recreation alters species composition of the scavenger assemblage and the ecological function of carrion removal. Outdoor recreation particularly

Table 1 Scavenger assemblage and carcass consumption patterns in El Hondo Natural Park, south-eastern Spain, in different types of Natural Park use (restricted area and public access area)

	Restricted area	Public access area	Total
Total species number	21	15	26
Bird species number	12	11	16
Mammal species number	8	4	9
Richness/carcass	1.1 ± 0.8	1.0 ± 0.9	1.1 ± 0.9
Abundance/carcass	1.2 ± 1.1	1.4 ± 1.7	1.3 ± 1.4
Detection time (h)	50.0 ± 59.9	45.2 ± 64.3	48.2 ± 55.4
Consumption time (h)	111.8 ± 134.7	157.5 ± 145.1	129.0 ± 127.3
Total consumed biomass (%)	85.1 ± 33.4	84.1 ± 31.9	84.7 ± 32.7
Vertebrate consumed biomass (%)	73.9 ± 42.4	52.2 ± 47.8	65.2 ± 45.8
Vertebrates presence (%)	90 (81.8)	53 (72.6)	143 (78.1)
Birds presence (%)	39 (36.4)	28 (38.3)	67 (37.2)
Mammals presence (%)	53 (48.2)	35 (47.94)	88 (48.1)
Non-native species presence (%)	13 (11.8)	31 (42.5)	44 (24.1)
Vertebrate totally consumed (%)	75 (68.2)	35 (46.7)	110 (60.7)

We show species number (for birds, mammals and total), richness/carcass (mean richness per carcass), abundance/carcass (mean abundance per carcass), detection time, consumption time, total consumed biomass (the percentage of carrion biomass consumed by vertebrates + invertebrates), vertebrate consumed biomass (the percentage of carrion biomass consumed only by vertebrates), vertebrate, bird and mammal presence (number of carcasses scavenged by vertebrates, birds or mammals, respectively), non-native species presence (number of carcasses scavenged by non-native species) and vertebrate totally consumed (number of carcasses consumed 100% by vertebrates). The table shows mean, ±SD. In the variables where brackets appear, the 'n' represents the number of carcasses in which vertebrate scavengers were recorded and the percentage in brackets (%).

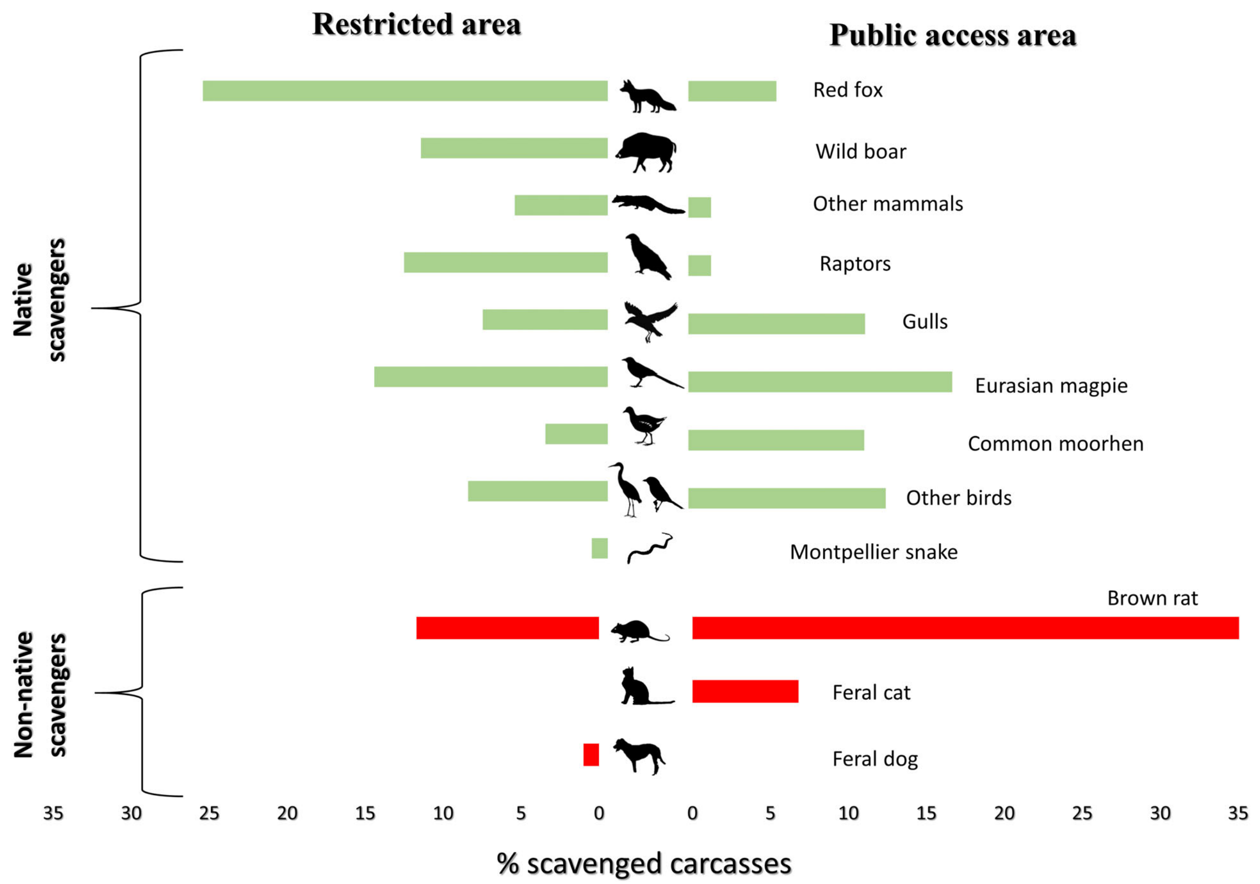

Figure 1 Percentage of carcasses scavenged by vertebrate scavengers in El Hondo Natural Park, south-eastern Spain, in restricted and public access areas. Native scavenger species are shown in green and non-native species in red.

Table 2 Results of the generalized linear models (GLMs) testing differences between types of Natural Park use (restricted area and public access area) in terms of richness, abundance, detection time, consumption time, total consumed biomass (proportion of biomass consumed by vertebrates + invertebrates) and vertebrate consumed biomass (proportion of biomass consumed only by vertebrates) of the vertebrate scavenger assemblage

	Coefficient	SE	*P*-value
Richness	−0.043	0.151	0.777
Abundance	0.153	0.135	0.256
Detection time	−0.151	0.252	0.550
Consumption time	0.578	0.256	**0.025**
Total consumed biomass	0.035	0.436	0.937
Vertebrate consumed biomass	−1.017	0.329	**0.002**

We show the coefficient of the model (Coefficient), the standard error (SE) and *P*-value. Significant *P*-values ($P < 0.05$) are in bold. All models include the weight of the carcass and the carcass type (fish, terrestrial bird, mammal or waterbirds) as a covariate. See Table S3 for covariate's details.

affected larger and more efficient scavenger species, which had a wide impact on carrion consumption patterns. In the public access area, we detected fewer vertebrate scavenger species contributing to consumption, these took longer to consume the carcasses and they consumed less carrion biomass. Furthermore, non-native species scavenged almost four times more carcasses in the public access than in the restricted area, evidencing that human activities promote the presence of non-native species (Reed & Merenlender, 2008; Gilby *et al*., 2022). It is well known that outdoor recreation affects wildlife in a number of different ways (Larson *et al*., 2016). Our results support our prediction evidencing how these human activities, in addition to altering the scavenging assemblage, also affect a key ecological process for the ecosystem.

Among the scavenger species, raptors were one of the groups most affected by outdoor recreation in our study area, as predicted by us. Many raptor species are known to be sensitive to habitat disturbance and human presence. For example, Perona, Urios, & López-López (2019) showed Bonelli's eagles *Aquila fasciata* travelled longer distances and spent more time away from their nest during weekends and holidays. Donázar, Ceballos, & Cortés-Avizanda (2018) proved that vehicle traffic and proximity to roads negatively affected the presence and richness of scavenger birds (raptors and crows), as well as carrion removal patterns. Similarly, Huijbers *et al*. (2013) recorded that raptors did not consume carrion in more urbanized coastal areas while they were the dominant species in more rural areas. We recorded raptors (greater spotted eagle and Eurasian marsh-harrier) feeding on 13% of the carcasses in the restricted area while the only raptor that consumed carrion in the public access area was the common kestrel *Falco tinnunculus*, at one carcass. Raptors feed during the day, temporally coinciding with human presence in natural areas. Moreover, larger birds show earlier flight response to human disturbances (Blumstein *et al*., 2005), raptors being particularly sensitive (Skagen, Knight, & Orians, 1991). These factors make outdoor recreation a much more serious threat to some vertebrate groups such as birds of prey.

Other group affected by outdoor recreation was that of native mammals, especially larger species such as red fox and wild boar. These species, together with raptors, consumed most of the carrion in the restricted area, however, the wild boar was absent and the red fox was recorded five times less feeding on carrion in the public access area (25.2 vs. 5.5%). Although there were no differences in species richness or mean abundance per carcass, nor in detection time, between the two types of Natural Park use, there was a clear difference in consumption time and the proportion of carrion consumed biomass by vertebrates, demonstrating the consumption efficiency of these key species once they have detected the carcass. However, it is important to notice that the proportion of the carcass consumed by vertebrates was more difficult to calculate and thus less accurate in the few carcasses where both vertebrate and invertebrate consumption were relevant. The absence or reduced presence of large species in the public access area may trigger cascading effects throughout wetland biodiversity (Crooks & Soulé, 1999). For example, generalist species such as the common moorhen, which is one of the main preys of the greater spotted eagle in this wetland (Pérez-García, Marco-Tresserras, & Orihuela-Torres, 2020), has appeared at three times more carcasses in the public access area, where its predators are much scarcer. In addition, the scarcity of the larger and more efficient carrion-consuming species in the public access area, together with human presence, which in turn leads to an increase in food waste from human origin, has led to the presence of non-native species at the carcasses, being four times higher than in the restricted area (Cunningham *et al*., 2018). This can negatively affect the entire wetland biodiversity, especially the bird community. In a study conducted in El Hondo Natural Park, rodents were found to be the main predators of eggs at nests of marsh-dwelling passerines (López-Iborra *et al*., 2004). In addition, El Hondo Natural Park has one of the largest European breeding population of the critically endangered marbled teal *Marmaronetta angustirrostris* and white-headed duck *Oxyura leucocephala*, for which brown rats and feral cats may pose a serious threat to their populations (Loss, Will, & Marra, 2013; authors unpublished data).

In addition to altering the vertebrate scavenger assemblage, we have shown that outdoor recreation alters the ecological process of carrion consumption and removal. Although the total consumed carrion biomass (vertebrates + invertebrates) is similar in the two types of Natural Park uses, the most efficient species avoid the public access area, the amount of carrion consumed by vertebrates is lower and the time that carrion prevails in the ecosystem increases, which has a number of consequences. On the one hand, the lower consumption of carrion by vertebrates promotes increased carrion consumption by invertebrates, so that recycling of nutrients along the food web changes, since nutrients are incorporated into the lower levels of the food web (Melis *et al*., 2007). In addition, vertebrates can transport nutrients over longer distances and move them between ecosystems, which makes them especially interesting in wetlands where they can play a key role in moving nutrients between the water–land interface by consuming fish carrion (Payne & Moore, 2006; Orihuela-Torres, Pérez-García, Sánchez-Zapata, Botella, & Sebastián-González, 2022; Orihuela-Torres, Sebastián-González, & Perez-García, 2022). On the other hand, as carrion is available for longer, it benefits the populations of 'feral' species such as cats, dogs and rats, which are in contact with humans, therefore, increasing the probability of disease transmission, triggering not only health problems, but also large economic costs (Markandya *et al*., 2008).

Conclusions

Outdoor recreation is increasing in PAs, especially in the wake of the COVID-19 lockdown, which has further increased the pressure on these areas (Primack & Terry, 2021). We have shown that outdoor recreation not only alters the terrestrial vertebrate scavenger assemblage in a Mediterranean wetland but it also negatively affects the consumption and removal of carrion, a key ecological ecosystem process, which highlights the urgency of regulating tourism in PAs. Our study also evidences that public access areas promote the presence in the ecosystem of non-native species which are more tolerant and benefit from human presence. In addition, these non-native species benefit from the fact that other larger, more human-elusive scavengers are scarcer in these areas, increasing the amount of carrion available to them and for longer periods of time (Cunningham *et al*., 2018). Raptors were one of the most affected groups. This is very interesting because their home range is very extensive and they can move all over the Natural Park, but they are reluctant to feed in the public access area. This wetland is an important wintering area for raptors, especially for some threatened species such as the greater spotted eagle, being its unique regular wintering area in Spain (Pérez-García, Marco-Tresserras, & Orihuela-Torres, 2020). Therefore, it is necessary to maintain areas restricted to visitors where these species can rest and feed to ensure the viability of their populations.

Although it is necessary and beneficial for human well-being to be in contact with nature (Naughton-Treves, Holland, & Brandon, 2005), PAs are refuges for biodiversity and are home to a large number of threatened species (Gray *et al*., 2016), so it is a priority to also maintain the ecological processes of the ecosystem to avoid the risk of these PAs becoming 'open-air zoos', where species need to be maintained by external inputs. To ensure biodiversity conservation in PAs, it is essential to maintain areas restricted to tourism (Reed & Merenlender, 2008). This is easy in large, uninhabited and inaccessible PAs, but it is highly complex and essential in areas that are easily accessible or close to anthropized areas where PAs tend to be smaller in size. In these small PAs, we encourage managers and conservationists to establish areas of restricted access aiming to serve as a refuge for the species most sensitive to human activities in order to preserve the ecological functions these species provide to the ecosystem.

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Author contributions

AOT, ESG and JMPG conceived the ideas and designed methodology; AOT, ESG and JMPG collected the data; AOT and ESG analysed the data; AOT, ESG and JMPG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Data Availability Statement

Data available via figshare https://doi.org/10.6084/m9.figshare.19697431.v7 (Orihuela-Torres, Sebastián-González, & Perez-García, 2022).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of carcasses scavenged by vertebrate scavenger species per type of Natural Park use (restricted area and public access area) and in total, in El Hondo Natural Park, south-eastern Spain. The table shows the number, and percentage in brackets (%) of carcasses at which they were recorded.

Table S2. Comparison of vertebrate scavenger assemblages, between types of Natural Park use (restricted area and public access area) by means of permutational multivariate analysis of variance (PERMANOVA). We show d.f. (degrees of freedom), SS (sum of squares), R2 (pseudo R2), *F* (pseudo *F*-statistic) and the *P*-value. Significant *P*-values ($P < 0.05$) are in bold.

Table S3. Results of the generalized linear models (GLMs) testing differences between types of Natural Park use (restricted area and public access area) in terms of richness, abundance, detection time, carcass consumption time, total consumed biomass (proportion of biomass consumed by vertebrates + invertebrates) and vertebrate consumed biomass (proportion of biomass consumed only by vertebrates) of the vertebrate scavenger assemblage in El Hondo Natural Park, south-eastern Spain. We show the coefficient of each model term, standard error (Std. error) and the *P*-value. Significant *P*-values ($P < 0.05$) are in bold.

Table S4. Scavenger assemblage and carcass consumption patterns in El Hondo Natural Park, south-eastern Spain, on different carcass types (fish, mammals, terrestrial birds and waterbirds) in terms of richness, abundance, detection time, carcass consumption time, total consumed biomass (proportion of biomass consumed by vertebrates + invertebrates) and vertebrate consumed biomass (proportion of biomass consumed only by vertebrates). We show the value and standard deviation (±SD).

Figure S1. Some recorded mammal vertebrate scavenger species in our survey in El Hondo Natural Park, Spain. (a) wild boar (Sus scrofa), (b) red fox (Vulpes vulpes), (c) brown rat (*Rattus norvegicus*), (d) common genet (*Genetta genetta*) and (e) feral cat (*Felis catus*).

Figure S2. Some recorded bird vertebrate scavenger species in our survey in El Hondo Natural Park, Spain. (a) Iberian grey shrike (*Lanius meridionalis*), (b) Eurasian magpie (*Pica pica*), (c) red-knobbed coot (*Fulica cristata*), (d) Eurasian coot (*Fulica atra*) and common moorhen (*Gallinula chlorophus*), (e) greater spotted eagle (*Clanga clanga*), (f) Eurasian jackdaw (*Corvus monedula*), (g) yellow-legged gull (*Larus michahellis*), (h) Eurasian marsh-harrier (*Circus aeruginosus*) and (i) Black-headed gull (*Chroicocephalus ridibundus*).