Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

The effect of COVID-19 confinement on the activity behaviour of red deer

Fernanda Garcia^{*,1}, António Alves da Silva², Helena Freitas³, José Paulo Sousa⁴, Joana Alves⁵

Centre for Functional Ecology (CFE), TERRA Associate Laboratory, Department of Life Sciences, University of Coimbra, Portugal

ARTICLE INFO

Keywords: Activity patterns COVID-19 Cultural services People outdoor activities Red deer

ABSTRACT

The COVID-19 pandemic has drastically affected people's social habits, especially those related to outdoor activities. We intended to understand the effects of the two national lockdowns in Portugal on the presence and activity of a wild population of red deer (Cervus elaphus) by analysing data from camera traps installed at Lousã mountain, in the central part of Portugal. The cameras were set between 2019 and 2021, and a total of 2434 individual contacts of red deer and 182 contacts of people were recorded. Results showed a higher human presence in the mountain area during the COVID-19 outbreak, especially during the first lockdown in 2020 (0.05 \pm 0.17 individuals/day), compared to the same period of the year before the pandemic (0.02 \pm 0.05 individuals/day), which resulted in an increase of people by 150%. The increase in human presence did not have a significant direct effect on the presence of red deer. Despite the low overlap of activity patterns between people and red deer, deer showed avoidance behaviour in the 24 h after the detection of human presence on camera traps, as well as an increase in daily activity during the 2020 lockdown, showing red deer's awareness of human visitation. These results showed that people's increased search for cultural services in wild environments during COVID-19 lockdowns, such as hiking and biking, seemed to influence the population of red deer, albeit momentarily.

1. Introduction

Recreational activities in natural environments, such as tourism, and visitation of mountains, parks, or rivers in more remote areas are classified as cultural services, which is a key ecosystem service for many people (Millennium Ecosystem Assessment, 2005). These are related to the experiences and non-material benefits people obtain from nature and are linked to cognitive development, spiritual enrichment, or aesthetic experiences (Millennium Ecosystem Assessment, 2005). The COVID-19 pandemic originated changes in

Received 7 December 2022; Received in revised form 18 May 2023; Accepted 25 May 2023

Available online 25 May 2023







^{*} Correspondence to: University of Coimbra, Centre for Functional Ecology (CFE), Department of Life Sciences, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal.

E-mail address: fernandagarcia377@gmail.com (F. Garcia).

¹ 0000-0001-8470-0693

² 0000-0001-9544-3936

³ 0000-0002-1907-9615

⁴ 0000-0001-8045-4296

 $^{^{5}}$ 0000-0003-2858-7803

https://doi.org/10.1016/j.gecco.2023.e02525

^{2351-9894/© 2023} The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

people's outdoor activity patterns, which may result in changes in their interactions with wildlife (e.g. Derks et al., 2020; Rutz et al., 2020; Cukor et al., 2021). Therefore, besides the direct effects on people's lives, either in terms of health or economically, the COVID-19 pandemic also had a pronounced impact on the ecosystems through the interaction between people and animals (e.g. Almeida and Santos, 2020; Lawler et al., 2021), which might lead to an increase in disturbance to wildlife. Human-wildlife interactions (Peterson et al., 2010) have often been associated with negative effects of animals on people, considering, for example, the negative impacts on agricultural crops or disease transmission, while the negative effects of people on wildlife have sometimes been disregarded. Nevertheless, several studies have been conducted to investigate the impact of tourism and/or outdoor activities performed by humans on wildlife (e.g. Jayakody et al., 2008, 2011; Kays et al., 2017).

Interactions between wildlife and humans may arise from the presence of people in natural areas, which may impact animal behaviour; for example, by turning them more nocturnal (Gaynor et al., 2018) or more afraid (Putman et al., 2017). Some studies reported changes in wildlife due to the pandemic, for example when animals were observed in cities or at hours they usually are not. Manenti et al. (2020) found evidence that several animal species were reported to change to a daily activity rather than being nocturnal, as well as occupying new habitats, as is the case of some rodents or porcupines. However, this topic has been discussed in the literature as a bit controversial since the effects could not be caused directly by a higher abundance of animals, but instead by people becoming more aware of their presence, or simply having more time or paying more attention to what is around them (Zellmer et al., 2020).

The lockdowns undoubtedly changed people's economic and societal patterns, providing unprecedented opportunities to understand people-animal interactions (Hunter, 2021). Nevertheless, studies evaluating issues other than human health-related problems are sparse (Usui et al., 2021), and quite contradictory results have been reported when evaluating the relationship between wildlife and humans because of the pandemic's lockdowns. During the pandemic, both positive (for example, the reduction of road kills (e.g. Bíl et al., 2021; Dörler and Heigl, 2021; García-Martínez-de-Albéniz et al., 2022; Łopucki et al., 2021; Pokorny et al., 2022, 2021)) and negative (as a result of the decrease in financial support and management actions (e.g. van der Merwe et al., 2021)) effects of humans on wildlife were reported around the world. Most of these studies, though, are qualitative or observational, mainly focusing on others' results or reports/news (e.g. Abd Rabou, 2020; Usui et al., 2021), and evidence from field work is still lacking (Rutz et al., 2020).

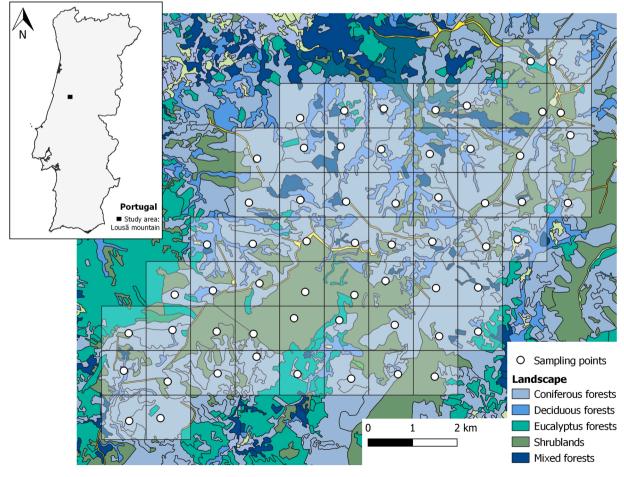


Fig. 1. Study area - Lousã mountain - and the 60 camera trap sampling locations.

Furthermore, most of the studies emphasize only one of the lockdowns, as argued by Pokorny et al. (2022), and barely focus on deer family (but see Jasińska et al., 2022).

We intend to understand the effects of the two lockdowns that occurred in Portugal in 2020 and 2021 on a wild population of red deer (*Cervus elaphus*) inhabiting the centre of Portugal by analysing both animal and human presence and activity. We expect that, since people were advised to stay at home, their presence in the Lousã mountain during these confinement periods would be lower, with positive consequences for the animals. We hypothesised that this decline in human disturbance would translate into behavioural changes in deer, e.g., more activity during daytime, and thus an increase in red deer detections by the camera traps. As humans can be perceived as predators (e.g., Frid and Dill, 2002; Jayakody et al., 2008, 2011; Ciuti et al., 2012), a decrease in human presence should result in a decrease in pressure for the animals, with a consequent increase in daily activities. If confirmed, such findings are expected to be a direct consequence of the decrease in people's presence on the mountain during lockdowns. Furthermore, since hunting is known to cause stress and behavioural changes in animals (Kilgo et al., 1998; Little et al., 2016; Vilela et al., 2020), the temporary suspension of legal hunting during the pandemic should also contribute to changes in the daytime activity of deer.

2. Materials and methods

2.1. Study area and red deer population

Our study was performed in the Lousã mountain, an area located in the central region of Portugal (Fig. 1). The mountain is characterized by a Mediterranean climate and has around 170 km^2 .

The red deer population under study is the result of a reintroduction program that occurred between 1995 and 1999, in which several animals were released on the mountain (Alves, 2013). This program aimed not only to enable big game hunting, but also to boost mountain tourism (Alves, 2013). Indeed, red deer are a charismatic species sought by ecotourists throughout the mountain and all-year-round, but especially during the rut season. Several tours can be done to see them, and hiking trails are present across the mountain.

The population of red deer is wild and has no natural predators. Yet, abandoned dogs act as non-natural predators, preying mostly on young and females. This population is hunted during traditional hunting events, called "montarias", which happen every year from October to February. During the pandemic, though, all hunting events were cancelled after March 24, 2020. In the 2020/2021 hunting season, "montarias" were allowed, but with several restrictions that led to a very low number of hunting events. The deer population was, therefore, free from legal hunting for almost two years (2020 and 2021).

In the study area, other species of wild ungulates are also present, including roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Domestic species such as goats (*Capra hircus*) with their shepherds can also be found within the study area.

2.2. Sampling design and data collection

The field work took place between March 2019 and March 2021. We considered four main sampling periods within these years. The first national confinement henceforth referred to as "lockdown 2020", comprises the period from March to June 2020. This sampling period was compared to the same period of the year before (March to June 2019), the spring of 2019 (before the SARS-CoV-2 pandemic), hereafter called "Spring before COVID-19". We also focused on the second national lockdown, called "lockdown 2021", from October 2020 to March 2021. This lockdown was likewise compared to the same period of the year before (before the SARS-CoV-2 pandemic), called "Winter before COVID-19" (October 2019 to March 2020). The lockdown periods in Portugal were characterized by people working remotely from home, with the exception of high priority jobs and other jobs that did not allow for remote work, and by travel restrictions, with the exception of medical appointments, supermarket visits, and small exercise activities, including walking dogs. Sampling periods took place in spring ("Spring before COVID-19" and "lockdown 2020") and winter ("Winter before COVID-19" and "lockdown 2021").

The study design consisted of 60 sampling points, separated from each other by approximately 1 km (Fig. 1). Twenty camera traps (Bushnell Natureview Cam HD: lens F=3.1 and FOV= 50° , trigger speed of 0.2 s, range of 19 m, and picture size of 14MP) were randomly placed in the study area in a rotation scheme to cover all the sampling points. The sampling points encompassed a diversity of habitats, and locations, including different human disturbances regarding trails, villages, and roads. All the sampling points, with the same camera location, were included in all the sampling periods. The rotation scheme consisted of 20 camera traps that were rotated every fifteen days so that all 60 sampling points were sampled within one and a half months (except during the confinement periods due to travel restrictions). During each visit, the SD card and batteries of each camera were changed, and the camera was moved. Each camera was programmed to take three photos every time the sensor was triggered. The cameras were placed at breast height, attached to a tree, and were active 24 h/day, registering the time, date, and temperature. The cameras recorded information on both animal and human presence. For each group recorded by the camera traps, the species to which it belongs, and the number of individuals were registered, as well as the day and time of each contact. Henceforward, the word "contact" refers to a recording of red deer or people by the camera trap (Wearn and Glover-Kapfer, 2017).

2.3. Statistical analysis

The photos obtained from the camera traps were inspected visually, identifying the species and the total number of individuals observed. The dataset contained the species, number of individuals, sampling point information, date, and time of each contact. Each

contact was considered independent when 10 min separated it from the previous contact (Akbaba and Ayaş, 2012; Marion et al., 2022). Results are presented as the number of individuals/day, which was calculated by dividing the number of contacts by the number of days sampled at each sampling period and sampling point.

A generalized linear mixed model (GLMM) with logistic binomial distribution was used to investigate differences between human presence on the mountain (dependent variable) on each sampling period (independent variable). In addition, another GLMM with logistic binomial distribution was used to test for the effect of people's presence (independent variable) on the presence of red deer (dependent variable) during the sampling periods. Sampling point was used as a random factor in both models.

Differences in red deer presence before and after the presence of people were also analysed. We analysed 6 periods with 24 h of duration meaning: [-72 h, -48 h], [-48 h, -24 h], [-24 h, 0 h] before human detection and]0 h, 24 h],]24 h, 48 h],]48 h, 72 h] after the human detection. In this specific case, we tested for the sampling points where the presence of people was detected, and therefore had an anthropogenic influence. However, 36 of the sampling points never recorded humans. We thus restricted our analyses on human influence to 24 sampling points for which we had records of human presence that were registered by the cameras. We obtained a total of 182 human individual contacts, with all of them considered in the analysis. Each human contact was linked to one of the six periods of 24 h, from which all red deer contacts 72 h, 48 h, and 24 h before and after human presence were analysed and used in subsequent analysis. A logistic binomial model was constructed considering the time influenced by the presence of people as an independent variable and red deer presence as a dependent variable, using the sampling points as a random factor. Pairwise multiple comparisons were performed using sequential Bonferroni correction for each dependent variable.

Significant values were considered at p < 0.05, and pairwise comparisons had a Bonferroni-adjusted alpha level. Results are presented as probabilities unless otherwise noted. Statistical analyses were performed using R 3.5.0 (R Core Team, 2019).

The spatial analysis of the number of red deer contacts and people contacts was performed through inverse distance weighted (IDW) interpolation maps (Wong, 2017), which was performed in QGIS 3.4.8.

The activity patterns and synchronization of activities between red deer and people were calculated following Ridout and Linkie (2009) through Kernel density analyses. The coefficient of overlap Δ , which varies between 0 (no overlap) and 1 (total overlap) was calculated and is represented by the grey area of the graph. Confidence intervals were calculated using bootstrapping. This statistical analysis was performed in R 3.5.0 (R Core Team, 2019) with the package "overlap" (Meredith and Ridout, 2014).

3. Results

We obtained 2434 individual contacts of red deer; 337 and 584 individual contacts of roe deer and wild boar, respectively; and 182 individual contacts of humans. A category named "others" was also considered, which included 862 individual contacts of several species, including foxes (*Vulpes vulpes*), pine martens (*Martes foina*) or domestic goats. Nevertheless, since our focus was on analysing the red deer–human interactions, the results will only consider these two species.

3.1. Sampling period and human's presence

The camera trap analysis showed an increased number of individuals/day of people during "Lockdown 2020" (Table 1), compared to the same period of the year before, representing an increase of 150%. "Lockdown 2021" had the lowest recordings in terms of individuals/day of people.

The probability of having people on the mountain area was significantly affected by sampling period (Wald $X^2 = 35.7$; df=3; p < 0.001), with humans being more likely to be present on the mountain during the "lockdown 2020" (0.004 ± 0.002) than in the "spring before COVID-19" (0.001 ± 0.0007) ($\beta = 1.051$; SE=0.291; z = 3.608; p < 0.001). Regarding "lockdown 2021", the probability of having people in the mountain (0.0007 ± 0.0004) was lower than in "winter before COVID-19" (0.001 ± 0.0007), although not statistically different ($\beta = -0.721$; SE=0.369; z = -1.958; p = 0.05).

When evaluating the influence of human presence on the presence of red deer, there was no effect ($\beta = -0.094$; SE=0.120; z = -0.782; p = 0.434).

However, there was a significant effect of human presence on the probability of red deer presence (Wald $X^2 = 27.091$; *df*=5; *p* < 0.001) when considering the time before and after human detection by camera-traps. The probability of red deer being present was highest in the period of [- 72 h, - 48 h[before human presence (0.28 ± 0.05), and lowest in the]0 h, 24 h] period, (0.09 ± 0.02) (Fig. 2). Significant differences were found when comparing the [- 72 h, - 48 h[with the [- 24 h, 0 h[(β = -1.235; SE=0.298; z = -4.146; *p* < 0.001) and]0 h, 24 h] after human detection by camera-traps (β = -1.295; SE=0.302; z = -4.285; *p* < 0.001).

Table 1

Mean number of individuals/day/sampling point ($\overline{x} \pm SE$) of red deer and people in the four sampling periods. ("Spring before COVID-19" is compared to "Lockdown 2020", and "Winter before COVID-19" to "Lockdown 2021").

	Spring before COVID-19	Lockdown 2020
Red deer (ind/day/sampling point)	0.34 ± 0.34	0.33 ± 0.34
People (ind/day/sampling point)	0.02 ± 0.05	0.05 ± 0.17
	Winter before COVID-19	Lockdown 2021
Red deer (ind/day/sampling point)	0.29 ± 0.42	0.30 ± 0.48
People (ind/day/sampling point)	0.02 ± 0.04	$\textbf{0.008} \pm \textbf{0.03}$

3.2. Spatial patterns

The increase in human presence during "lockdown 2020" was noticed in specific locations across the study area, represented by the hotspots on the map (in red, Fig. 3). This increase was most noticeable near national roads, trails, or villages, all of which are easy for people to get to. Red deer showed slight spatial adjustments along the sampling periods (Fig. 3).

3.3. Temporal patterns

Analysing the activity patterns, it is apparent that red deer and human activities practically did not overlap (Fig. 4). Red deer showed marked activity patterns, with peaks of activity at sunrise and sunset. On the other hand, people were active mostly during the daytime, with peaks of activity after sunrise and before sunset (Fig. 4).

During "lockdown 2020" the overlap between red deer and people was the highest observed, although it was still low ($\Delta = 0.34$). "Spring before COVID-19" and "lockdown 2021" presented the lowest overlap values, both with $\Delta = 0.28$ (Fig. 4).

4. Discussion

Our results showed that humans altered their daily activities during the COVID-19 pandemic. Unlike our predictions, we found that people were frequenting the mountain area more than usual during the first lockdown, in 2020, when compared to the same period of the year before (without pandemic). This was unexpected since people had travel restrictions and were supposed to stay at home during lockdown periods. However, they also had more time available and looked for different types of recreation, although it implied breaking some rules of confinement, which might explain such an unexpected increment in camera traps recording people. Other studies also found an increased number of visitors in forested areas during the 2020 lockdown (Cukor et al., 2021; Derks et al., 2020; Venter et al., 2020), which highlights the importance of natural areas for people, during this time. This increase in human sightings was notorious in specific locations, and it was not found during the confinement period of 2021, probably since the lockdown in 2020 took place in spring while the 2021 confinement occurred in the winter.

Although our results showed a significant increase in human presence in the Lousa mountain area during the 2020 lockdown, when we analysed the effects of people's presence on the presence of red deer, the results showed that there was no significant effect. Red deer did, however, show a significant avoidance behaviour that lasted for 24 h after human contact, while slightly increasing their diurnal activities in lockdown 2020. People increased their presence mostly in places near trails, villages, or asphalt roads that were previously associated with negative effects on wildlife (Fletcher et al., 1999; Miller et al., 2001; Taylor and Knight, 2003; Oliveira, 2018).

The red deer avoidance behaviour is not only a reflection of the increase in people in the mountain but may also be a result of the predation risk associated with humans (e.g., Chassagneux et al., 2019, 2020). Although people can be perceived as a threat even if performing non-lethal activities, such as recreational ones (Frid and Dill, 2002), they are also seen as a threat associated with hunting. The presence of humans has been reported as changing feeding behaviour, leading to differential habitat use, and an increase in vigilance in several species (Miller et al., 2001; Stankowich, 2008; Szwagrzyk et al., 2020; Tost et al., 2020; Zanette and Clinchy, 2017) and in red deer more specifically (Ciuti et al., 2012; Jayakody et al., 2008, 2011; Möst et al., 2015). Even though legal hunting events were cancelled in the study area during the COVID-19 pandemic, predation history (the ghost of predators past) might well explain the

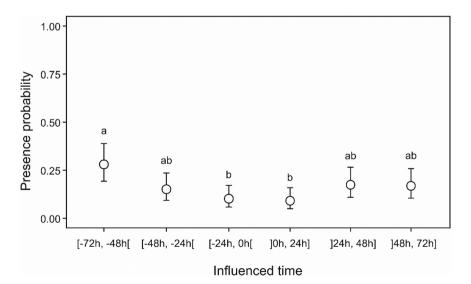


Fig. 2. Probability of red deer's presence ([-72 h, -48 h], [-48 h, -24 h], [-24 h, 0 h]) before and after (]0 h, 24 h],]24 h, 48 h],]48 h, 72 h]) human detection by camera-trap (0). Different lower-case letters denote significant differences (p < 0.05).

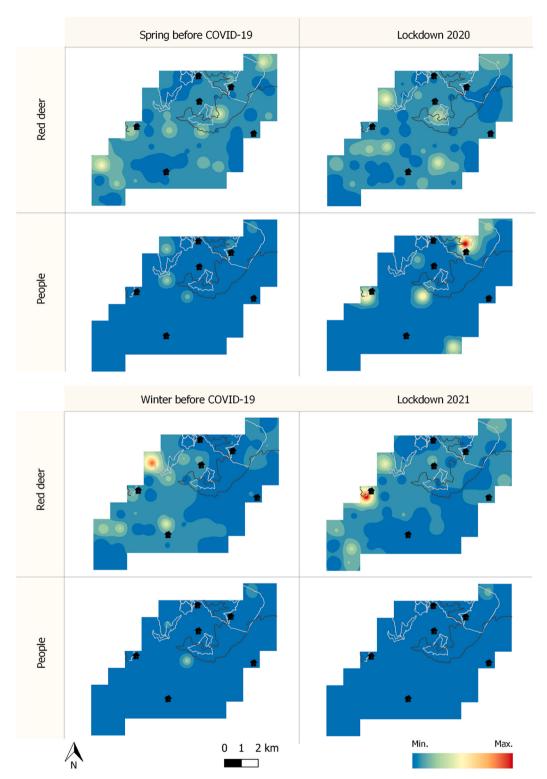


Fig. 3. Inverse distance weighted (IDW) interpolation map of the number of individuals/day of red deer (max. 3.25 individuals/day) and people (max. 1 individual/day) during the four sampling periods. Black lines represent the national roads that cross the mountain, white lines are the pedestrian paths/trails, and the house symbols represent the villages. ("Spring before COVID-19" is compared to "Lockdown 2020", and "Winter before COVID-19" to "Lockdown 2021").

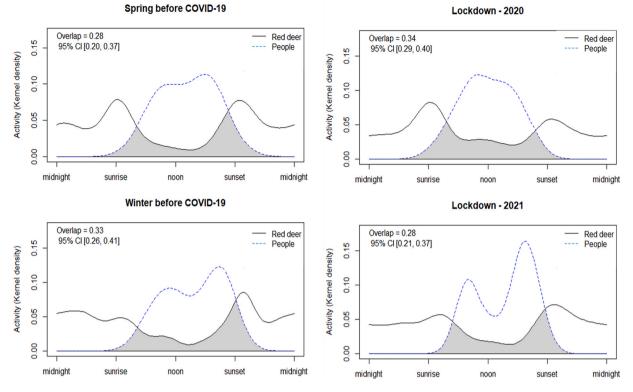


Fig. 4. Activity patterns of red deer and people and their overlap (grey area), during the four sampling periods ("Spring before COVID-19" is compared to "Lockdown 2020", and "Winter before COVID-19" to "Lockdown 2021").

avoidance behaviour of red deer, as animals are known to remember responses to predators for several decades (e.g., Li et al., 2011).

Besides avoiding the 24 h after human presence, we actually showed that red deer may exhibit avoidance behaviour even before the detection of people by the camera. Although unexpected, this result may indicate that the presence of people starts to happen before their detection by camera-traps, making red deer perceive them and adjust their behaviour. As so, red deer seems to be sensitive to the increase in movement and presence of people in their surroundings. After the avoidance period, however, red deer presence seemed to increase again. As this red deer population is quite accustomed to non-lethal human presence in the study area (as in Kays et al., 2017 and Marion et al., 2022), especially during recreational activities, or the rut, deer might adjust more quickly after disturbance.

Regardless of the overall low overlap of activity between red deer and people, red deer showed an increase in daily activity in the noon hours that was not common before the pandemic, neither in spring nor in winter. This increase in daily activity was very noticeable in lockdown 2020. It was likely caused by people disturbing the red deer, which caused them to move and trigger the cameras more than they normally do at this time of day, when they are laying down and ruminating. This change in activity can be seen precisely as a response to predators (humans) (Sibbald et al., 2011). During lockdown 2021, on the other hand, there was no such increase in daily activity, which could be corresponding to the lower presence of people captured on cameras in the mountain area. Even though hunting was still allowed in the winter before COVID-19, and contrarily to our expectations, the results did not show an increase of red deer activity during daytime. This might be explained by the fact that most hunting activities in the winter before COVID-19 occur in the surroundings of the mountain area, and not in the core of our study area.

It is possible to observe differences between the general bimodal activity pattern (that is also known as an anti-predator strategy, being the animals' crepuscular) between sampling periods from spring and winter. The peaks of activity during winter sampling periods were less pronounced than those during spring. This might be explained by lower human presence (Kamler et al., 2007), but most likely by the effect of the season of the year, which leads to activity adjustments independently of human presence. Indeed, depending on the time of year, red deer are known to have altitudinal movements and to change their activity patterns according to their biological stage, adjusting the periods of activity and time spent in each activity or behaviour, depending, for example, on the duration of daylight and temperature (Berger et al., 2002; Relvas, 2020; Prebanić and Ugarković, 2015).

Overall, our results demonstrate that, on the one hand, red deer are accustomed to non-lethal human presence, as shown by the increase in their presence after 24 h of people's presence, but that the unexpected increase in human presence at the mountain area during the lockdown 2020 affected red deer's spatial and activity patterns. Therefore, awareness-raising actions directed at visitors and recreational hunters are crucial to mitigate disruptions to wildlife (Mancini et al., 2020). A balance between recreational activities and wildlife populations is essential to maintain the welfare of all species and ecosystem service provision, avoiding thus human-wildlife conflicts and enabling better coexistence (Malo et al., 2011).

5. Conclusions

Our results showed an increase in recreational activities in the Lousã mountain during the 2020 lockdown, compared to the previous homologous period. In some places, this intensification of the human presence was accompanied by an increase in red deer detections by camera traps during the diurnal hours. This is probably a reflection of the red deer's awareness of people's presence, since it led animals to move more during those hours they are usually laying. An avoidance behaviour by red deer was also noticed, especially in places near villages, roads, and trails. The avoidance behaviour lasted for 24 h after human presence. These responses of red deer might have been triggered by the unexpected increase of people recreating in the mountain as well as their predator history. Notwithstanding, although these effects seem to be momentary with no long-term effects, for conservation and management purposes it is important to raise awareness of the relevance of wildlife and ecosystems to human welfare, helping them to maintain a good relationship with nature and avoiding conflicts.

Funding

This study was funded by the Portuguese Foundation for Science and Technology (FCT) by the fellowship of A. Alves da Silva (SFRH/BD/75018/2010) and F. Garcia (SFRH/BD/131627/2017). J. Alves was supported by a the strategic plan of the Centre for Functional Ecology - Science for People and the Planet (CFE) (UIDP/04004/2020), and by the contract 2022.05848.CEEIND, both financed by FCT/MCTES through national funds (PIDDAC). The study was carried out under the project "F4F - Forest for Future - Pilot project for the constitution of a regional network for the valorisation of the forest sector in the Central Region. PP6 – MyFORESt (CENTRO-08-5864-FSE-000031)", co-financed by the Regional Operational Programme Centro 2020, Portugal 2020, and the European Union, through the European Social Fund (ESF). This study was also funded by Instituto do Ambiente, Tecnologia e Vida from Faculdade de Ciências e Tecnologia da Universidade de Coimbra (IATV-UC), the strategic plan of the Centre for Functional Ecology - Science for People and the Planet (CFE) (UIDB/04004/2020), and Associate Laboratory TERRA (LA/P/0092/2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Acknowledgments

We would like to acknowledge Sandra Simões, Rubén Mina, Sofia Relvas, Maria Inês Mendes and Inês Silva for their valuable help during the field work. We also thank to the anonymous reviewers and Editor for their constructive comments on the manuscript. A special acknowledgment to Prof. Dr. Kathreen Ruckstuhl for the English revision.

References

- Abd Rabou, A.F.N., 2020. How is the COVID-19 outbreak affecting wildlife around the world. ? Open J. Ecol. 10, 497–517. https://doi.org/10.4236/oje.2020.108032. Akbaba, B., Ayaş, Z., 2012. Camera trap study on inventory and daily activity patterns of large mammals in a mixed forest in north-western Turkey. Mammalia 76, 43–48. https://doi.org/10.1515/MAMM.2011.102.
- Almeida, F., Santos, J., 2020. The effects of COVID-19 on job security and unemployment in Portugal. Int. J. Sociol. Soc. Policy 40, 995–1003. https://doi.org/ 10.1108/LJSSP-07-2020-0291.

Alves, J., 2013. Ecological Assessment of the Red Deer Population in the Lousa Mountain (Thesis). University of Aveiro,

- Berger, A., Scheibe, K., Brelurut, A., Schober, F., Streich, W., 2002. Seasonal variation of diurnal and ultradian rhythms in red deer. Bio. Rhythm. Res 33, 237–253. https://doi.org/10.1076/brhm.33.3.237.8259.
- Bíl, M., Andrášik, R., Cícha, V., Arnon, A., Kruuse, M., Langbein, J., Náhlik, A., Niemi, M., Pokorny, B., Colino-Rabanal, V.J., Rolandsen, C.M., Seiler, A., 2021. COVID-19 related travel restrictions prevented numerous wildlife deaths on roads: A comparative analysis of results from 11 countries. Biol. Conserv 256. https://doi. org/10.1016/j.biocon.2021.109076.
- Chassagneux, A., Calenge, C., Siat, V., Mortz, P., Baubet, R., Saïd, S., 2019. Proximity to the risk and landscape features modulate female red deer movement patterns over several days drive hunts. Wildl. Biol. https://doi.org/10.2981/wlb.00545.
- Chassagneux, A., Calenge, C., Marchand, P., Richard, E., Guillaumat, E., Baubet, R., Saïd, S., 2020. Should I stay or should I go? Determinants of immediate and delayed movement responses of female red deer (*Cervus elaphus*) to drive hunts. PLoS ONE 15. https://doi.org/10.1371/journal.pone.0228865.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS One 7, 1–13. https://doi.org/10.1371/journal.pone.0050611.
- Cukor, J., Linda, R., Mahlerová, K., Vacek, Z., Faltusová, M., Marada, P., Havránek, F., Hart, V., 2021. Different patterns of human activities in nature during Covid-19 pandemic and African swine fever outbreak confirm direct impact on wildlife disruption. Sci. Rep. 11, 1–11. https://doi.org/10.1038/s41598-021-99862-0. Derks, J., Giessen, L., Winkel, G., 2020. COVID-19-induced visitor boom reveals the importance of forests as critical infrastructure. Policy Econ. 118, 1–5. https://doi.
- Derks, J., dessen, L., winker, G., 2020. COVID-19-induced visitor boom reveals the importance of forests as critical infrastructure. Poincy econ. 116, 1–5. https://doi.org/10.1016/j.forpol.2020.102253.
- Dörler, D., Heigl, F., 2021. A decrease in reports on road-killed animals based on citizen science during COVID-19 lockdown. PeerJ 9. https://doi.org/10.7717/ peerj.12464.

Fletcher, R.J., Mckinney, S.T., Bock, C.E., 1999. Effects of recreational trails on wintering diurnal raptors along riparian corridors in a Colorado grassland. J. Raptor Res. 33, 233–239.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6. https://doi.org/10.5751/es-00404-060111.

García-Martínez-de-Albéniz, Í., Ruiz-De-villa, J.A., Rodriguez-Hernandez, J., 2022. Impact of COVID-19 lockdown on wildlife–vehicle collisions in NW of Spain. Sustainability 14. https://doi.org/10.3390/su14084849.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 1979 360, 1232–1235. https://doi.org/10.1126/science.aar7121.

Hunter, P., 2021. COVID-19 and the opportunities for research. EMBO Rep. 22, 1-4. https://doi.org/10.15252/embr.202152757.

Jasińska, K., Krauze-Gryz, D., Gryz, J., 2022. Changes in roe deer (*Capreolus capreolus*) daily activity patterns in Warsaw during the COVID-19 pandemic. Eur. Zool. J. 89, 870–876. https://doi.org/10.1080/24750263.2022.2096130.

Jayakody, S., Sibbald, A., Gordon, I., Lambin, X., 2008. Red deer Cervus elaphus vigilance behaviour differs with habitat and type of human disturbance. Wildl. Biol. 14 (1), 81–91. https://doi.org/10.2981/0909-6396(2008)14[81:RDCEVB]2.0.CO;2.

Jayakody, S., Sibbald, A., Mayes, R., Hooper, R., Gordon, I., Lambin, X., 2011. Effects of human disturbance on the diet composition of wild red deer (*Cervus elaphus*). Eur. J. Wildl. Res 57, 939–948. https://doi.org/10.1007/s10344-011-0508-z.

Kamler, J., Jędrzejewska, B., Jędrzejewski, W., 2007. Activity patterns of red deer in Białowieża national park, Poland. J. Mammal. 88, 508–514. https://doi.org/ 10.1644/06-MAMM-A-169R.1.

Kays, R., Parsons, A., Baker, M., Kalies, E., Forrester, T., Costello, R., Rota, C., Millspaugh, J., McShea, W., 2017. Does hunting or hiking affect wildlife communities in protected areas. J. Appl. Ecol. 54, 242–252. https://doi.org/10.1111/1365-2664.12700.

Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behavior of white-tailed deer: Implications for conservation of the Florida panther. Conserv. Ecol. 12, 1359–1364. https://doi.org/10.1111/j.1523-1739.1998.97223.x.

Lawler, O., Allan, H., Baxter, P., Castagnino, R., Tor, M., Dann, L., Hungerford, J., Karmacharya, D., Lloyd, T., López-Jara, M., Massie, G., Novera, J., Rogers, A., Kark, S., 2021. The COVID-19 pandemic is intricately linked to biodiversity loss and ecosystem health. Lancet Planet Health 5, 840–850. https://doi.org/ 10.1016/S2542-5196(21)00258-8.

Li, C., Yang, X., Ding, Y., Zhang, L., Fang, H., Tang, S., Jiang, Z., 2011. Do Père David's deer lose memories of their ancestral predators? PLoS One 6, 1–6. https://doi.org/10.1371/journal.pone.0023623.

Little, A.R., Webb, S.L., Demarais, S., Gee, K.L., Riffell, S.K., Gaskamp, J.A., 2016. Hunting intensity alters movement behaviour of white-tailed deer. Basic Appl. Ecol. 17, 360–369. https://doi.org/10.1016/j.baae.2015.12.003.

Łopucki, R., Kitowski, I., Perlińska-Teresiak, M., Klich, D., 2021. How is wildlife affected by the covid-19 pandemic? Lockdown effect on the road mortality of hedgehogs. Animals 11, 1–8. https://doi.org/10.3390/ani11030868.

Malo, J.E., Acebes, P., Traba, J., 2011. Measuring ungulate tolerance to human with flight distance: A reliable visitor management tool. Biodivers. Conserv 20, 3477–3488. https://doi.org/10.1007/s10531-011-0136-7.

Mancini, F., Leyshon, B., Manson, F., Coghill, G.M., Lusseau, D., 2020. Monitoring tourists' specialisation and implementing adaptive governance is necessary to avoid failure of the wildlife tourism commons. Tour. Manag 81. https://doi.org/10.1016/j.tourman.2020.104160.

Manenti, R., Mori, E., di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G.F., Rubolini, D., 2020. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. Biol. Conserv 249. https://doi.org/10.1016/j. biocon.2020.108728.

Marion, S., Demšar, U., Davies, A.L., Stephens, P.A., Irvine, R.J., Long, J.A., 2022. Red deer behavioural response to hiking activity: a study using camera traps. J. Zool. 317, 249–261. https://doi.org/10.1111/jzo.12976.

Meredith, M., Ridout, M., 2014. Overlap: estimates of coefficient of overlapping for animal activity patterns. R package version 0.2 4.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being. Island Press, Washington, DC. https://doi.org/10.5822/978-1-61091-484-0_1.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124-132.

Möst, L., Hothorn, T., Müller, J., Heurich, M., 2015. Creating a landscape of management: Unintended effects on the variation of browsing pressure in a national park. Ecol. Manag. 338, 46–56. https://doi.org/10.1016/j.foreco.2014.11.015.

- Oliveira, R., 2018. Avoidance Behaviour of Wild Ungulates to Roads: Its Effects on Spatial Distribution, Habitat Use and Activity Patterns (Thesis). University of Coimbra.
- Peterson, M., Birckhead, J., Leong, K., Peterson, M., Peterson, T., 2010. Rearticulating the myth of human-wildlife conflict. Conserv. Lett. 3, 74–82. https://doi.org/ 10.1111/j.1755-263X.2010.00099.x.

Pokorny, B., Cerri, J., Bužan, E., 2021. Roadkill in a time of pandemic: the analysis of wildlife-vehicle collisions reveals the differential impact of COVID-19 lockdown over mammal assemblages. EcoEvoRxiv 1–37.

Pokorny, B., Cerri, J., Bužan, E., 2022. Wildlife roadkill and COVID-19: a biologically significant, but heterogeneous, reduction. J. Appl. Ecol. 59 (5), 1291–1301. https://doi.org/10.1111/1365-2664.14140.

Prebanić, I., Ugarković, D., 2015. Analysis of seasonal activities of red deer (*Cervus elaphus* L.) in relation to the mating season, lunar phases and air temperature. Russ. J. Ecol. 46, 393–395. https://doi.org/10.1134/S1067413615040153.

Putman, B.J., Drury, J.P., Blumstein, D.T., Pauly, G.B., 2017. Fear no colors? Observer clothing color influences lizard escape behavior. PLoS One 12, 1–13. https://doi.org/10.1371/journal.pone.0182146.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria: Available at: (https://www.R-project.org/).

Relvas, S.M., 2020. Testing the Activity Budget Hypothesis to Explain Sexual Segregation in Red Deer (Thesis). University of Coimbra,

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/ 10.1198/jabes.2009.08038.

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 4, 1156–1159. https://doi.org/10.1038/s41559-020-1237-z.

Sibbald, A., Hooper, R., McLeod, J., Gordon, I., 2011. Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers, 817.825 Eur. J. Wildl. Res 57. https://doi.org/10.1007/s10344-011-0493-2.

Stankowich, T., 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biol. Conserv 141, 2159–2173. https://doi.org/10.1016/j. biocon.2008.06.026.

Szwagrzyk, J., Gazda, A., Muter, E., Pielech, R., Szewczyk, J., Zięba, A., Zwijacz-Kozica, T., Wiertelorz, A., Pachowicz, T., Bodziarczyk, J., 2020. Effects of species and environmental factors on browsing frequency of young trees in mountain forests affected by natural disturbances. Ecol. Manag. 474. https://doi.org/10.1016/j. foreco.2020.118364.

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963. https://doi.org/10.1890/1051-0761 (2003)13[951:WRTRAA]2.0.CO;2.

Tost, D., Strauß, E., Jung, K., Siebert, U., 2020. Impact of tourism on habitat use of black grouse (*Tetrao tetrix*) in an isolated population in northern Germany. PLoS One 15, 1–19. https://doi.org/10.1371/journal.pone.0238660.

Usui, R., Sheeran, L.K., Asbury, A.M., Blackson, M., 2021. Impacts of the COVID-19 pandemic on mammals at tourism destinations: a systematic review. Mamm. Rev. 51, 492–507. https://doi.org/10.1111/mam.12245.

van der Merwe, P., Saayman, A., Jacobs, C., 2021. Assessing the economic impact of COVID-19 on the private wildlife industry of South Africa. Glob. Ecol. Conserv 28. https://doi.org/10.1016/j.gecco.2021.e01633.

- Venter, Z.S., Barton, D.N., Gundersen, V., Figari, H., Nowell, M., 2020. Urban nature in a time of crisis: recreational use of green space increases during the COVID-19 outbreak in Oslo, Norway. Environ. Res. Lett. 15. https://doi.org/10.1088/1748-9326/abb396.
- Vilela, S., da Silva, A.A., Palme, R., Ruckstuhl, K.E., Sousa, J.P., Alves, J., 2020. Physiological stress reactions in red deer induced by hunting activities. Animals 10, 1–14. https://doi.org/10.3390/ani10061003.

Wearn, O., Glover-Kapfer, O., 2017. WWF Conservation technology series 1(1). WWF-UK, Woking, United Kingdom.

- Wong, D., 2017. Interpolation: inverse-distance weighting. International encyclopedia of geography, 15vol set: people, the earth, environment and technology, 1. John Wiley & Sons,
- Zanette, L.Y., Clinchy, M., 2017. Predator–prey interactions: Integrating fear effects. In: APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior. American Psychological Association, pp. 815–831. https://doi.org/10.1037/0000011-039.
- Zellmer, A.J., Wood, E.M., Surasinghe, T., Putman, B.J., Pauly, G.B., Magle, S.B., Lewis, J.S., Kay, C.A.M., Fidino, M., 2020. What can we learn from wildlife sightings during the COVID-19 global shutdown? Ecosphere 11. https://doi.org/10.1002/ecs2.3215.