Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 33 (2): 166–171, 2022
OPEN ACCESS
Available online at:
http://www.italian-journal-of-mammalogy.it
doi:10.4404/hystrix-00557-2021

Research Article

COVID-19 lockdown splits activity peaks of two mesopredators and potentially relaxes interspecific competition in rural habitat

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Keywords:
Vulpes vulpes
Martes foina
interspecific competition
human disturbance
tourist pressure

Article history:
Received: 10 May 2022
Accepted: 11 October 2022

Acknowledgements
We would like to thank G. Bujko for his help in the field work. We are grateful to K. Schmidt for sharing part of the data and T. Kamiński for help in organizing data from camera traps. We would also like to thank Białowieża National Park for providing data about the number of tourists who visited the Nature and Forest Museum. Special thanks go to T. Samojlik for creating drawings of the marten and the fox.

Abstract

COVID-19 lockdown has provided a unique example of a sudden and significant reduction of human presence in a rural area, especially in villages with high tourist pressure. We used camera-trapping to investigate the effect of reduction of human activity due to COVID-19 lockdown in a rural area on activity patterns of species considered urban exploiters and urban adapters. The activity patterns of both predators changed slightly and activity peaks shifted without significant differences in temporal niche overlap. The stone marten, an urban exploiter, had a bimodal activity pattern and shifted the main peak of its activity earlier during COVID-19 lockdown. It was quick to respond to the decrease in human presence in the first half of the night by increasing activity in that time. Meanwhile, the red fox, an urban adapter, showed larger variation in activity patterns and shifted summer and autumn-winter activity peaks to later at night or even early morning. These changes resulted in slight differences in the overlap of activity rhythms of both species. Stone marten and red fox have adapted their activity to avoid human encounter and are active mainly at night, responding by a small extent to reduction of human presence during COVID-19 lockdown, which occurs mainly during the day. However, COVID-19 lockdown and lower human mobility may partially reduce interspecific competition induced by anthropogenic activities in rural areas.

Introduction

The period of unusual reduction of human mobility caused by COVID-19 lockdown, referred to as "anthropause" (Rutz et al., 2020) or "COVID-19 quietus" (Montgomery et al., 2021), created the opportunity to analyse the linkage between human pressure with animal behaviour. Wild animals were quick to respond to such a drastic and sudden event by looking for food and roaming in areas previously dominated by humans (Bar, 2021). Researchers have hypothesized that free-living animals may respond to COVID-19 lockdown by changes in activity schedules and vocalizations, increasing densities, decreasing vigilance, different movement dynamics, use of new resources and increasing exploratory behaviour (Montgomery et al., 2021). Animals adapted to inhabiting urbanized areas are likely to be the most susceptible to these changes. Meta-analysis of 62 species showed that mammals have increased their nocturnality in response to human disturbance (Gaynor et al., 2018) and some mammals may become more diurnal in response to human lockdown (Montgomery et al., 2021; Behera et al., 2022; Jasińska et al., 2022).

Various species respond differently to environmental changes caused by urbanization and human activity (e.g. McKinney, 2002). "Urban avoiders" are the first species to decline in the proximity of humans because of changes in habitat caused by urbanization; "urban adapters" have partially reduced their fear of humans and can utilize human subsidies within suburban areas, but predominantly rely on natural resources outside cities and villages. Finally, "urban exploiters" are almost completely dependent on human subsidies and occur more frequently inside than outside manmade environments such as cities and villages (McKinney, 2002). In environments created by humans, we may expect these last two groups of animals to change their circadian activity pattern in relation to human activity in various ways and to have different responses to decreased human presence. While urban adapters are likely to change their activity with the decrease of human disturbance, the latter is expected to have a lower impact on urban exploiters. However, studies of the influence of human disturbance on animal activity in urban and rural areas are limited due to the permanent and often high occurrence of humans in these habitats. COVID-19 lockdown unusually reduced human mobility and provided the opportunity to analyse wildlife in cities and villages with reduced human activity. This should be especially visible in sites (cities and villages) visited by tourists, where, at least in some seasons, the number of people can increase by 2–4 times.

The stone marten (*Martes foina*) and red fox (*Vulpes vulpes*) are two mesopredators adapted to habitats modified by humans and occur in cities and villages throughout the whole year (Duduś et al., 2014; Handler et al., 2020; Jackowiak et al., 2021; Wereszczuk and Zalewski, 2015). Both species inhabit a wide variety of habitat types within their geographic range, along a gradient from natural areas, through rural farmlands, to centres of cities (Bateman and Fleming, 2012). However, in Białowieża Primeval Forest, NE Poland, the stone marten uses built-up areas only (Wereszczuk and Zalewski, 2015), which makes it an urban exploiter in this region, while the red fox within our study area mainly utilizes forests (Jędrzejewski and Jędrzejewska, 1992). The red fox may also be found in villages and, therefore, can be considered as an urban adapter. The stone marten seems to be better adapted to urbanized areas than the red fox (Duduś et al., 2014) as it colonised the most highly urbanized part of the cities as well as large villages. Stone marten body size — smaller than that of the red fox — and its climbing ability (Baghli et al., 2002; Serafini and Lovari, 1993) enable martens to use buildings as resting sites and shelters during high human activity in the daytime.

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Red foxes, with their larger size and terrestrial lifestyle, need a cover against people to rest in, therefore they utilise suburban areas in cities (Duduś et al., 2014). Both species are omnivorous-feeders and may explore various sources of food, including that which is provided by humans — fruits in gardens or food waste (Czernik et al., 2016; Handler et al., 2020). To avoid interaction with people, both species are mostly nocturnal or crepuscular (Kammerle et al., 2020; Wereszczuk and Zalewski, 2015), but in some regions red fox activity showed a cathemeral pattern (Ikeda et al., 2016) and its plasticity in circadian activity is larger than the stone marten's (e.g. Monterroso et al., 2014).

Białowieża Primeval Forest (BPF) is one of the largest forest complexes in Europe and one of its last non-altered habitats (Samojlik et al., 2013), visited by about 165000 tourists (average for 2018–2019) every year. The largest part of BPF (about 80%) is managed by the State Forests Holding which is a commercial timber production-oriented entity with little focus on biodiversity conservation (Mikusiński and Niedziałkowski, 2020). The remaining part of BPF, which constitutes the national park, is not exploited for timber and all other human uses are restricted to its southwestern part. The village of Białowieża and the adjacent village of Podolany cover a total area of 1170 ha (information from the municipal office). The villages are located in the centre of the forest complex and are directly surrounded by abandoned fields in succession, meadows, and valleys of streams. Villages have developed infrastructure to accommodate a large number of visitors while being permanently inhabited by about 1 830 people (Polska w liczbach, 2020). On 12$^{\text{th of}}$ March 2020, Poland initiated a lockdown in response to the COVID-19 pandemic that lasted 80 days. The next lockdowns, in winter 2020/2021 and spring 2021, lasted 85 and 72 days, respectively. The number of tourists from Poland and other countries visiting BPF has decreased since then. In contrast to urban green areas, where human pressure increased during COVID-19 lockdown (Venter et al., 2021), BPF is distant from cities and human pressure, and the number of tourists decreased during lockdown.

In this paper, we test whether the COVID-19 lockdown, which caused a reduction of the number of tourists visiting Białowieża village and a reduction in villagers' mobility, can affect the circadian activity pattern of the stone marten and the red fox. We expect that the decreased number of humans in the village will (1) change the activity pattern of the stone marten only slightly, as this species can be classified as a urban exploiter; but (2) the red fox, as an urban adapter, will increase its activity during the period of low human activity, especially before midnight; and (3) those changes will result in lower overlap of activity patterns of both species.

Material and methods

Camera trapping

We placed camera traps in Białowieża and Podolany villages using from 13 to 36 camera traps at a time; 20 out of the 36 deployed worked continuously during the study period (except for short breaks due to breakdown, theft, or necessity of rearranging), and the rest worked continuously for at least four months. Both villages are mainly composed of narrow private properties, one adjacent to another, usually with a house and a barn or other buildings on each property. Camera traps were placed on private properties, often in the vicinity of buildings, in abandoned barns which could be accessed by both predators, as well as near roads in the park situated within the village (Fig. 1). In order to increase detectability, we positioned the camera traps next to paths, against the walls of buildings, in compost sites or other locations more frequently used by wild animals (based on our knowledge from winter snow or telemetry tracking observations). Camera traps were set up in open areas within the property, which ensured good visibility within the cameras' range all year round. We placed them at 50–100 cm from the ground in order to capture stone marten and red fox movement. We used digital trail cameras (SGN-5220) triggered by passive infrared sensors with a detection angle of 35 °C and range of 20 m. Detection launched 40 s videos with 1 s time lag. We defined the independence interval between successive captures as five minutes of consecutive records of individuals of the same species (Negrões et al., 2010; Podolski et al., 2013).The Moran's *I* autocorrelation coefficient (Paradis and Schliep, 2019) indicated no spatial correlation in the number of observations at camera trap locations for stone marten (Moran's I=-0.14, p=0.07) and red fox (Moran's I=0.05, p=0.32). All observations were recorded in Central European Summer Time (CEST; UTC+02:00). Videos were collected continuously throughout the years 2018–2021. Camera trap data was organized and classified using TRAPPER software (Bubnicki et al., 2016). Maps were created using the package `tmap` (Tennekes, 2018) with orthophotomap for the study area downloaded using the package `rgugik` (Dyba and Nowosad, 2021) and for the continent from Geoportail France (https://www.geoportail.gov.fr).

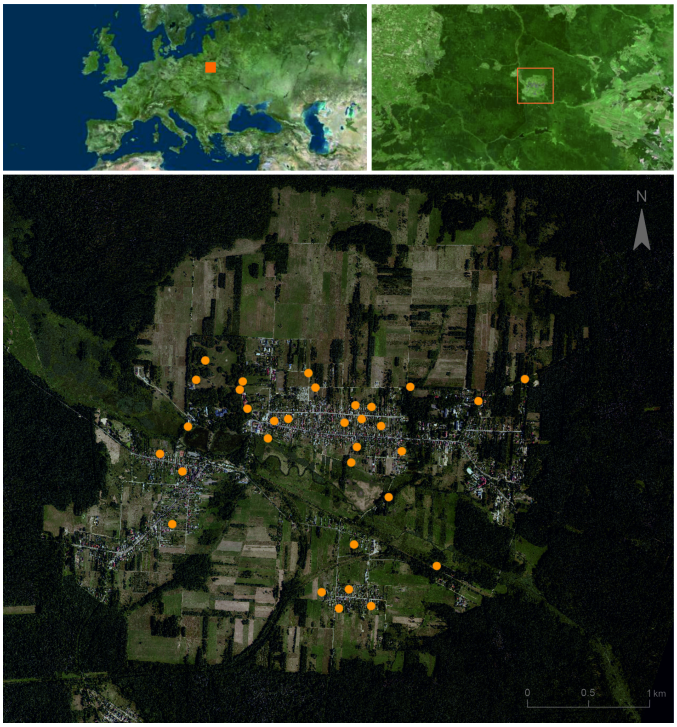

Figure 1 – Study area and locations of camera traps (N=36) in the villages of Białowieża Primeval Forest, NE Poland, in 2018–2021.

Restrictions

The first pandemic restrictions were introduced on the 12$^{\text{th}}$ of March, when schools, cultural institutions and restaurants were closed. This was the beginning of a series of increasing restrictions, with the period of the most intensive lockdown in Poland occurring between the 1$^{\text{st}}$ and the 20$^{\text{th}}$ of April 2020. In this time, restrictions to free movement were introduced, and there was no access to forests, including urban green areas, natural reserves, commercial forests and national parks. All restrictions were lifted by the end of May 2020 (Związek Przedsiębiorców i Pracodawców, 2021). In the next year, restrictions were imposed from 20 March in the form of closures of schools, cultural institutions, sport facilities, restaurants and hotels. These restrictions were lifted between the 19$^{\text{th}}$ of April and the end of May 2021 (Service of the Republic of Poland, 2021a, 2021, May 12). The lockdown in the autumn-winter season was continued from 28 December 2020 to 17 January 2021, but restrictions in the fields of education, economy and social life were introduced from 24 October (Service of the Republic of Poland, 2021c).

Statistical analyses

We combined collected data into two periods: pre-lockdown (2018–2019) and COVID-19 lockdown (2020–2021) and divided each of them into three seasons: spring (March-May), summer (June-September) and autumn-winter (October-February). Seasons have been divided according to the biology of both species, as behaviour of martens and foxes in spring is related to cub rearing, while in the summer (the mat-

Table 1 – The overall number of animal observations and the number of stone marten and red fox independent observations recorded in subsequent seasons in Białowieża village and the number of camera trap stations in two periods : pre-lockdown (2018–2019) and during COVID-19 lockdown (2020–2021).

Years	Season	Total no. observations	No. independent observations		No. camera trap stations
			Stone marten	Red fox	
2018–2019	spring	2122	305	33	
	summer	2234	426	35	15–16
	autumn-winter	4273	914	174	
2020–2021	spring	3291	302	207	
	summer	821	393	27	13–36
	autumn-winter	3242	456	90	

ing period of the stone marten), and in the autumn-winter period, individuals of both species are mostly solitary (Genovesi et al., 1997; Herr et al., 2008). The measure of human impact — the number of monthly tourists who visited the Nature and Forest Museum of Białowieża National Park from January 2018 to August 2021 (data collected by Białowieża National Park) — was presented in three seasons and two periods: pre– and during lockdown. The number of tourists who visited the museum does not reflect the overall impact of tourists (not all tourists visiting Białowieża Forest visited the museum) but has been used as a relative indicator of human influence which varied in proportion to its overall impact.

To estimate overlap of activity patterns between the periods before and during lockdown in three seasons we used a kernel density analysis and calculated the coefficient of overlap (Δ *Dath*), which varies from 0 (no overlap) to 1 (complete overlap) (Ridout and Linkie, 2009). We used the Δ *Dath4* coefficient (an estimator recommended for samples with $n>75$; Meredith and Ridout, 2021) for the stone marten dataset, and Δ *Dath1* for the red fox dataset due to smaller sample size. We calculated 95% confidence intervals for the overlap coefficient from 10 000 bootstrap samples using the function `bootCIlogit`. These analyses were carried out with the package `overlap` (Meredith and Ridout, 2021; Ridout and Linkie, 2009). To test the significance of differences, the activity distributions of each pair were compared by performing the Wald test using the function `compareAct` from the package `activity` (Rowcliffe, 2021). Statistical analyses were carried out in R version 4.0.3 (R Core Team, 2020).

Results

In total, 15983 videos with animal observations were collected, of which 2796 and 566 were independent observations of the stone marten and the red fox, respectively (Tab. 1). The average number of tourists decreased during COVID-19 lockdown by 89% in spring, 32% in summer and 76% in autumn-winter (declined by 5166, 3269 and 1815 tourists, respectively; Pearson's χ^2=2294.6, p<0.001; Fig. 2). The lowest overall number of tourists visited BPF in the winter and the highest in the summer.

The stone marten had a bimodal pattern of activity during all seasons in both periods. Daily activity patterns of stone marten were not significantly different between pre– and during COVID-19 lockdown periods. The coefficient of activity overlap between the two periods was 0.92 (95% CI: 0.85–0.98; p=0.78) in spring, 0.90 (95% CI: 0.83–0.96; p=0.24) in summer, and 0.92 (95% CI: 0.86–0.97; p=0.48) in autumn-winter. However, the peak of its activity in spring shifted from 23:00 pre-lockdown to 20:00 during lockdown (Fig. 3). Similarly, the peak of stone marten activity shifted from 01:00 pre-lockdown to 18:00 during lockdown in autumn-winter (Fig. 3). In summer, during the pre-lockdown period, marten displayed an activity pattern with two similar peaks, the first around 20:00 and the second around midnight, but during the COVID-19 lockdown period, the first peak of activity was higher, showing a similar increase of activity to the two other seasons.

The activity patterns of the red fox changed between the period pre- and during lockdown more than the stone marten's, but not significantly. The coefficient of overlap between the two periods was 0.80 (95% CI: 0.63–0.97; p=0.26) in spring, 0.83 (95% CI: 0.73–0.93; p=0.72) in summer, and 0.73 (95% CI: 0.60–0.87; p0.11) in autumn-winter. The red fox started its activity earlier in spring (but the peak of its activity remained at about 1:00), while during autumn-winter it was more active after midnight; its activity peak shifted from 1:00 pre-lockdown to 4:00 during lockdown (Fig. 3). The red fox displayed a bimodal pattern of activity during the summer, with one peak around 17:00–21:00 and the other around 1:00, the first being the main peak pre-lockdown and the other during lockdown (Fig. 3).

The activity overlap between the stone marten and red fox was high in all seasons with a Δ ≥0.66, and there was no significant difference between periods of pre- and COVID-19 lockdown (Fig. 4). In the spring lockdown, the period of the greatest reduction in the number of tourists, the coefficient of overlap was higher (pre-lockdown: Δ=0.66, 95% CI: 0.46–0.85, p=0.11; during lockdown: Δ=0.79, 95% CI: 0.70–0.89, p=0.70). In summer and autumn-winter, the coefficient of overlap was higher pre-lockdown than during the lockdown period (summer pre-lockdown: Δ=0.88, 95% CI: 0.81–0.96, p=0.41; summer lockdown: Δ=0.76, 95% CI: 0.65–0.87, p=0.08; autumn-winter pre-lockdown: Δ=0.84, 95% CI: 0.77–0.9, p=0.25; autumn-winter lockdown: Δ=0.72, 95% CI: 0.60–0.85, p=0.17; Fig. 4). The main peaks of activity of the two species were separate in almost every season during COVID-19 lockdown.

Discussion

We investigated the effect of reduction in human disturbance during the COVID-19 lockdown on activity patterns of species considered urban adapters and urban exploiters. We showed that the stone marten and the red fox changed their activity patterns during lower human activity only slightly, mainly by altering activity peaks, especially the urban

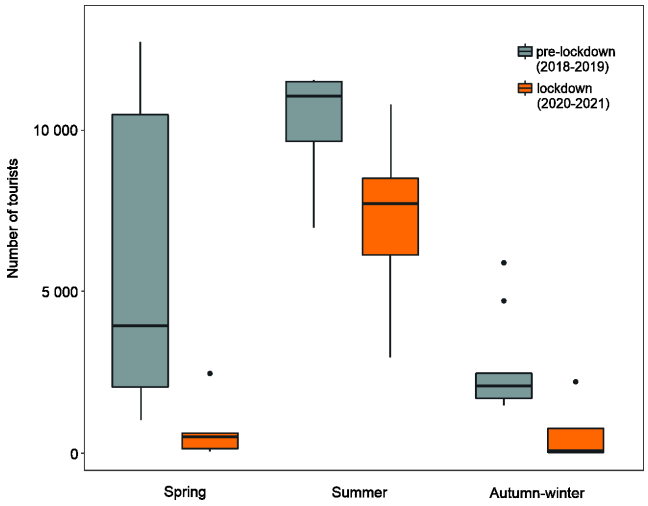

Figure 2 – Seasonal average monthly number of visitors to the Nature and Forest Museum of Białowieża National Park, pre- and during COVID-19 lockdown. Difference between number of tourists in pre-lockdown and lockdown over seasons was significant (Pearson's χ^2=2294.6, p<0.001).

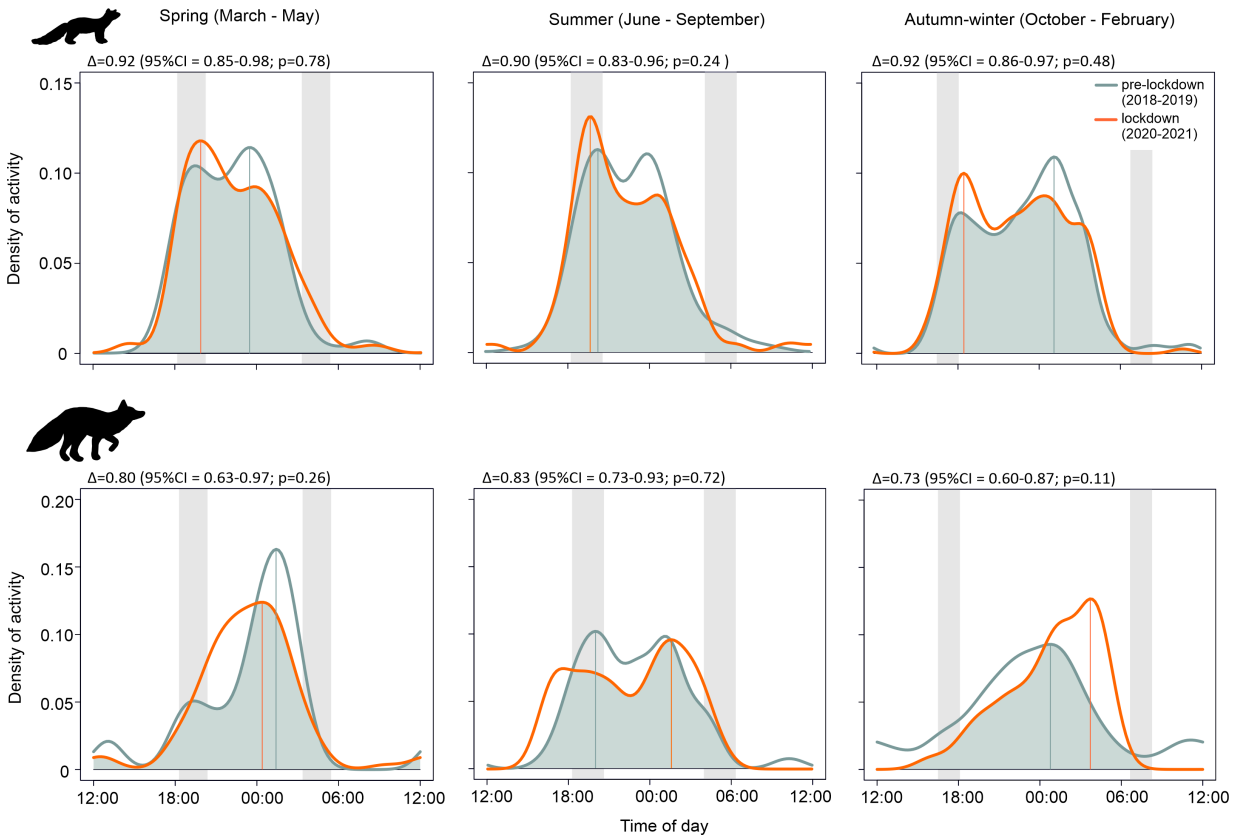

Figure 3 – Seasonal patterns of diel activity in the stone marten (*Martes foina*, upper panel) and the red fox (*Vulpes vulpes*, lower panel) pre-lockdown and during COVID-19 lockdown. Grey and orange lines indicate kernel density estimates, dark grey areas represent overlap of temporal activity between pre-lockdown and COVID-19 lockdown periods, and light grey shaded areas represent sunrise and sunset periods in each season. Estimated overlap (Δ) is shown with 95% CI and *p*-value from Wald test for the significance of differences in the activity distributions of each pair.

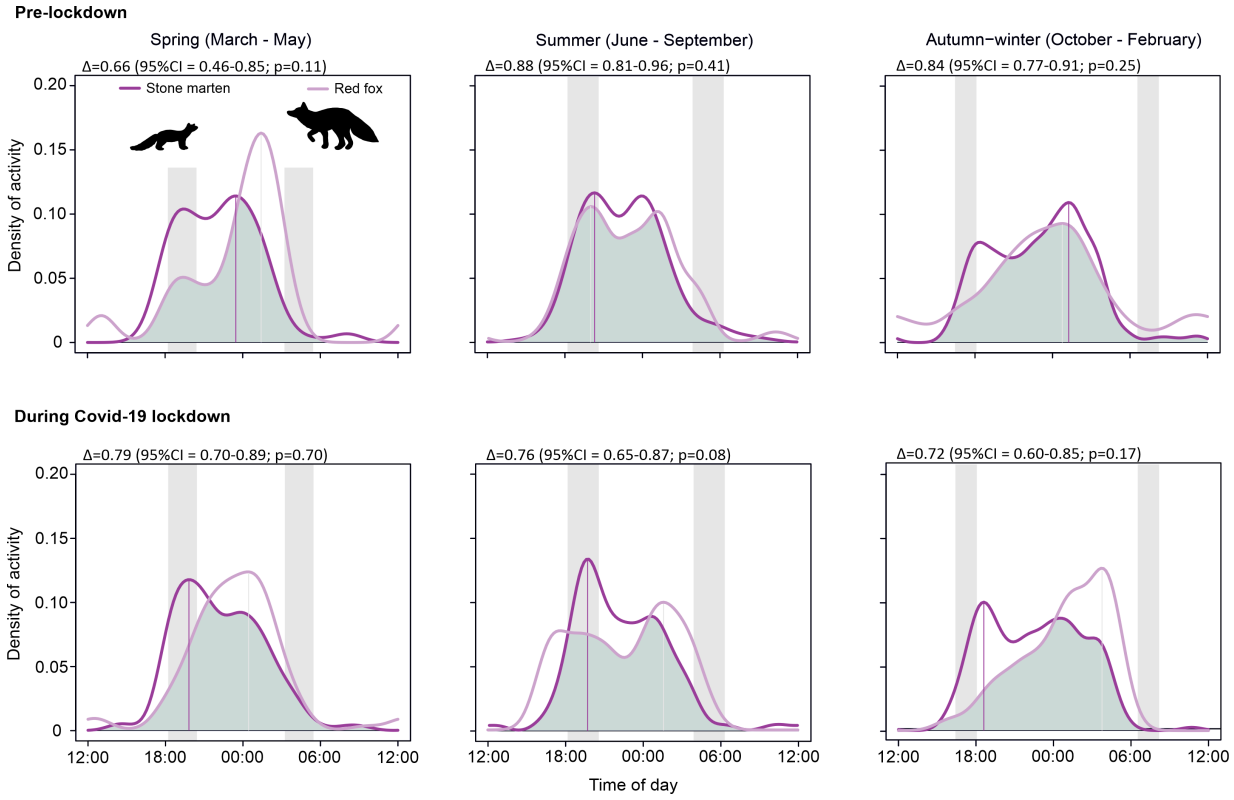

Figure 4 – Comparison between daily activity patterns of the stone marten (*Martes foina*) and red fox (*Vulpes vulpes*) over pre-lockdown (2018–2019) and during COVID-19 lockdown periods. Purple and lavender lines indicate kernel density estimates for stone marten and red fox respectively, the dark grey area represents overlap of temporal activity between both predators, and light grey shaded areas represent sunrise and sunset periods in each season. Estimated overlap (Δ) is shown with 95% CI and *p*-value from Wald test for the significance of differences in the activity distributions of each pair.

exploiter, i.e. the stone marten, which shifted its activity peak to an earlier time. In consequence, the change in activity overlap of these species was insignificant between periods. However, activity peaks were more separated in COVID-19 lockdown, potentially relaxing interspecific competition.

Martens and foxes avoided periods of high human activity during hours of daylight, and the activity patterns of both predators were mainly nocturnal (Kammerle et al., 2020; Roy et al., 2019). These findings confirm previous results concerning activity patterns of both predators in urban and rural areas (Díaz-Ruiz et al., 2016; Pandolfi et al., 1997; Posillico et al., 1995). Our data are consistent with telemetry data analysing the temporal pattern of stone marten activity in Białowieża (Wereszczuk and Zalewski, 2015). The number of tourists in Białowieża village dropped during lockdown from 5796, 10359 and 2395 to 630, 7089 and 579 in spring, summer and autumn-winter, respectively, providing a unique example of a sudden and significant reduction of human pressure in a rural area. Spring lockdown and the summer after lockdown resulted in the greatest decrease of the total number of tourists in BPF, while autumn-winter did not have such an effect because of the already small number of tourists, even before the lockdown. However, contrary to our expectations, neither of the species increased their activity during daylight hours.

The small changes in activity pattern of both predators in years of higher and lower human presence suggest that the permanent presence of the relatively low number of inhabitants of the Białowieża district (11 people/km^2; Polska w liczbach, 2020) is sufficient to affect animal behaviour. The further increase of human population only slightly modified both predators' activity pattern. On the other hand, the length of the lockdown period may have been too short for the predators to change their behaviour, although other studies indicate that even a very short period of limiting human presence affects behavioural change (Behera et al., 2022; Jasińska et al., 2022). Fixed times of starting and ending diurnal activity of stone marten and red fox, also during COVID-19 lockdown, seem to confirm long-term adaptation to minimize encounters with humans and a constant level of vigilance. Stone martens have adapted to occupy habitats in proximity of human settlements over several thousand years (Anderson, 1970). For example, as an adaptive response to avoid human encounter, the marten's activity was demonstrated to end by 6:00 based on radio-telemetry data (Wereszczuk and Zalewski, 2015). Despite reduced numbers of tourists, it is likely that the constant presence of inhabitants did not allow for a significant change in the activity of this urban exploiter species. Thus, only minor changes were observed during lockdown, probably because the anthropause reflected the human mobility level observed a few decades ago (Rutz et al., 2020). In addition, animals that had previously adapted their activity to avoid humans and are active mainly at night, when human activity is minimized, may not respond to reduction of human presence during the day. This is in contrast to species with daily activity, which adjusted their activity depending on whether human activity increased or decreased during COVID-19 lockdown (Lewis et al., 2021; Manenti et al., 2020; Olejarz et al., 2021; Jasińska et al., 2022).

In all seasons, the stone marten (urban exploiter species) had a relatively stable bimodal activity pattern in periods pre- and during COVID-19 lockdown, the only difference being a shift in peaks of main activity. When looking at the pre-lockdown period, the second peak in stone marten activity (at about midnight) was higher in contrast to COVID-19 lockdown, when the first peak (between 18:00–19:00) was markedly higher. Similar plasticity was observed in other areas where stone martens were active in the night-time but locally adapted their strategies, which was expressed as a shift in activity peak in response to environmental cues (Monterroso et al., 2014). The decrease of human presence and reduced noise in the first half of the night-time caused martens to quickly respond with an increase in activity during that time, suggesting that martens benefit from crepuscular activity. It is likely that after 12 hours of rest during the daylight hours, martens are "starvation driven" and they need to find food earlier at night (Cozzi et al., 2012), which is made possible by the lowered probability of encountering humans during COVID-19 lockdown.

The activity patterns of the red fox (urban adapter species) varied more with the seasons and periods without a constant pattern. This may partly be related to the lower number of observations than for the stone marten. Foxes in the rural area around the Białowieża Forest started activity during crepuscular hours and showed a concentration of activity during the night, in line with previous research from urbanized areas (Kammerle et al., 2020). As an adaptation to higher human disturbance, predators reduced morning activity and increased their night-time activity (Gálvez et al., 2021; Wang et al., 2015). For example, red foxes utilized habitats outside built-up areas, like parks and cemeteries, early in the night when humans were still active and changed to more built-up areas when human presence was lower there during the second part of the night (Gloor, 2002). Similarly, Białowieża village is surrounded by meadows where red foxes may be active before they enter the village. However, we were unable to detect them using camera traps, which were located only in the village. The overlap of activity patterns of the red fox before and during lockdown in three analysed seasons were high but lower than the activity patterns of stone marten. The lowest overlap was in autumn-winter when the red fox shifted their early morning activity peak. The red fox used urbanized areas when human activity was the lowest and avoided periods of high human activity more than the stone marten (Capon et al., 2021). At the same time, as urban adapters, red foxes are not strictly related to landscapes modified by humans (McKinney, 2002) and show some tolerance of humans outside built-up areas, e.g. in places used for recreational purposes (Lewis et al., 2021).

The COVID-19 lockdown affected activity overlap of the stone marten and the red fox only slightly. Temporal niche overlap between the species before and during COVID-19 lockdown was high. Similarly, the high level of their niches overlap has been demonstrated in previous studies conducted in urbanised areas with high human disturbance (Petrov et al., 2016; Roy et al., 2019; Torretta et al., 2017). Mammals inhabiting rural and urban areas avoid times of the day when humans are most active (Barrueto et al., 2014; Gaynor et al., 2018), whereby overlap of activity patterns among mesocarnivores has increased (Gálvez et al., 2021). However, the temporal partitioning of activity is an important strategy used by subordinate carnivores to avoid the risk of injuries or death associated with higher risk of encountering a large predator (Hunter and Caro, 2008; Palomares and Caro, 1999). Niche partitioning is a multidimensional dynamic process, and an increase in overlap of one niche dimension may be compensated by a decrease of another (Schoener, 1974); human disturbance can alter at least two dimensions — the temporal (Gaynor et al., 2018) and thropic niches of mesocarnivores (Manlick and Pauli, 1992). Thus, the probability of interspecific competition in human-dominated landscapes increased (Donadio and Buskirk, 2006). Although we did not confirm lower temporal niche partitioning of mesocarnivores during COVID-19 lockdown, we showed a segregation of their activity peaks suggesting that periodic reduction of human disturbance may alter their activity in anthropogenic areas. For this reason, COVID-19 lockdown and lower human mobility may have decreased human-induced interspecific competition after the relaxation of restrictions.

Conclusions

Our results showed that the stone marten and the red fox, which represent urban adapters and urban exploiters, have adapted to avoid human encounters by restricting their activity to the night-time. COVID-19 lockdown and the lower number of people at that period changed the human pressure on both predators' night-time activity only slightly; therefore, the activity patterns of these species changed to a low extent. Stone marten activity patterns were more stable between periods and less affected by human presence, while the red fox's activity pattern showed larger variation between periods. In consequence, the overlap between the stone marten and the red fox was reduced during COVID-19 lockdown, which suggests that presence of human as a top predator may enhance temporal niche overlap between these mesopredators. In general, lower pressure of human disturbance allowed animals to forage

at preferred times, when they were not frightened by people, resulting in at least partly relaxed interspecific competition.

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Associate Editor: N. Fattorini