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ORIGINAL ARTICLE

Temporal partitioning among native and alien lagomorphs and their predator: insights into coexistence mechanisms from long-term camera trapping

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Abstract

The introduction of alien species can alter existing species interactions and behaviours, posing new challenges for wildlife conservation and management. Long-term data provide an invaluable resource for testing theoretical principles and understanding species' responses to new colonisers. In this study, we used camera-trap data to assess temporal partitioning among two lagomorphs—the native European hare (*Lepus europaeus*) and the alien Eastern cottontail (*Sylvilagus floridanus*), a rabbit species native to Northern and Central America—and their principal predator, the red fox (*Vulpes vulpes*), before and after the Eastern cottontail colonised the study area. Our results reveal that, in both phases, the European hare and the red fox exhibited a low degree of temporal overlap. The red fox showed predominantly nocturnal activity, whereas the hare consistently showed a strongly bimodal pattern with peaks around sunrise (or early morning) and sunset. This temporal partitioning appears to be a key mechanism by which the European hare minimises encounters with the red fox, thereby reducing predation risk. The arrival of the Eastern cottontail did not modify the hare's diel activity patterns, while the red fox exhibited subtle shifts in its activity rhythms, possibly reflecting adaptive foraging in response to changing prey availability. The Eastern cottontail showed seasonal behavioural plasticity in its activity rhythm, being predominantly nocturnal during the cold season and shifting to a bimodal pattern with a marked peak in the early morning (one hour preceding that of the European hare) during the warm season. In the cold season, when resource scarcity may force the cottontail to occupy the same spatial locations at a fine scale, temporal overlap with the native lagomorph was lower. We suggested that temporal segregation with the European hare is a key mechanism allowing the Eastern cottontail to establish in the invaded area. These findings underscore the role of temporal behavioural plasticity in mediating interspecific interactions and facilitating the success of alien species such as the Eastern cottontail.

Keywords Diel activity pattern · Hare · Cottontail · Mammal · Temporal partitioning · Temporal segregation

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Introduction

Spatial and temporal segregation are key behavioural mechanisms through which species with similar ecological niches, i.e. potentially competing species, may coexist in sympatry (Monterroso et al. 2016, 2020; Torretta et al. 2017; Burgos et al. 2023). This may occur in case of limited resources (e.g. resting sites, nesting sites, trophic resources) due to exploitative competition, whereby the use of a resource by one species reduces its availability for other species, forcing them to utilise the same (or suboptimal) resource at different locations or times (Chen et al. 2019; Corlatti et al. 2019). Additionally, independently of resource availability,

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interspecific interference competition can prevent or reduce access to resources by other species. In this form of competition, individuals of one species actively dominate a resource through direct interactions, thereby promoting segregation or partitioning along spatial or temporal axes (Ferretti et al. 2011; Petroelje et al. 2021). Body size has often been invoked as one of the main factors affecting the outcome of these negative interactions, with larger species tending to dominate over smaller species (Peters 1983; Palomares and Caro 1999; Donadio and Buskirk 2006; Chock et al. 2018), although this pattern is not universal (Martin and Ghalambor 2014). A relevant context to investigate interspecific spatiotemporal segregation in nature occurs when a species appears in a range where it was naturally absent, potentially triggering interspecific competition (Stolle et al. 2015; Merson et al. 2019; Ferretti and Mori 2020). This is the case of alien species that, due to human activity, are becoming a relevant threat to biodiversity at any scale, from local to global (IPBES 2019).

The Eastern cottontail (*Sylvilagus floridanus*) (Lagomorpha: Leporidae) is a small rabbit (0.9–1.8 kg, Amori et al. 2009) native to Northern and Central America, which has been introduced to multiple European countries for hunting purposes since the 1950s (Scalera et al. 2016), despite being established only in Italy (Dori et al. 2019). In Italy, the Eastern cottontail appeared in the 1960s (Mussa et al. 1996). Currently, the largest populations occur in north-western Italy, but small scattered populations are also present in central Italy (Dori et al. 2019). The spread of the Eastern cottontail increases concerns about the conservation status of the European hare (*Lepus europaeus*), which is a native lagomorph widely distributed across the peninsula (Vidus-Rosin et al. 2010, 2011). It also raises concerns about the potential transmission of several native pathogens through its role as a vector (Tizzani et al. 2007; Lavazza et al. 2015; Zanet et al. 2013).

The European hare is a lagomorph distributed throughout Eurasia (Averianov et al. 2003) where it represents an important prey species for several mammal carnivores as well as for birds of prey (Fattorini et al. 2018; Hackländer and Schai-Braun 2018). This species mostly selects agroecosystems, where it uses open farmland for feeding, and shrubs, hedgerows, and woodlands for resting and nesting (Neumann et al. 2011; Schai-Braun and Hackländer 2014; Mori et al. 2022). Currently, the European hare is widely spread in Europe, where local introductions have also occurred for hunting purposes, even outside its native range (Barbar and Lambertucci 2018). However, the European populations have been declining in several parts of their range due to habitat loss, fragmentation, and degradation, illegal hunting, parasite-mediated disease, and environmental pollution (Edwards et al. 2000; Smith et al. 2005; Gortazar et al. 2007; Mori et al. 2022).

The introduced Eastern cottontail is a potential competitor of the European hare due to the use of similar macrohabitats to forage, nest, and rest, even though a finer habitat selection at the microscale has been suggested as a mechanism to avoid competition under sympatric conditions (Vidus-Rosin et al. 2012; Bertolino et al. 2013). Furthermore, the arrival of the Eastern cottontail may disrupt prey-predator relationships in meso-mammal communities (Balestrieri et al. 2005). It may also negatively affect the European hare due to increased predation pressure from the red fox *Vulpes vulpes* (Cerri et al. 2017). The red fox is a generalist and opportunistic mammal mesopredator and is one of the most widely distributed carnivores in the world (Hoffman and Sillero-Zubiri 2021). In Europe, it is one of the main predators of lagomorph species, with consumption rates that increase in anthropogenic environments and at lower latitudes, likely reflecting the higher availability of lagomorphs in these contexts (Soe et al. 2017).

Understanding mechanisms that allow the coexistence of these two lagomorph species is thus essential to plan adequate conservation strategies aimed at preserving European hare populations and to limit the spread of the alien Eastern cottontail. Studies conducted under sympatric conditions are pivotal to investigate intraguild spatiotemporal segregation and interactions between preys and predators. While some studies on habitat selection have been developed under sympatric conditions—providing insights into spatial overlap or segregation (Bertolino et al. 2011, 2013; Vidus-Rosin et al. 2012)—no studies have investigated diel activity rhythms in sympatry. Current knowledge about the activity patterns for the Eastern cottontail is derived from research where the European hare is not present. In its introduced range, the cottontail mainly shows nocturnal activity, consistent with its diel activity in its native range (Andrade-Ponce et al. 2022; Mori et al. 2022). While diel activity patterns are inherently regulated by genetic mechanisms (King and Takahashi 2000; Ko and Takahashi 2006) and the species' endogenous clock (Kronfeld-Schor and Dayan 2003), several external abiotic and biotic factors can fine-tune daily routines (Arias-Del Razo et al. 2011). Indeed, the cottontail has shown a notable degree of behavioural plasticity, being able to adjust its activity by exploiting crepuscular hours as a putative mechanism to avoid encounters with nocturnal predators (red fox, feral or free-ranging domestic cat *Felis catus*) (Panzeri et al. 2021). The diel temporal activity of the Eastern cottontail likely overlaps substantially with that of the European hare, which is primarily nocturnal and crepuscular (Viviano et al. 2021; Mori et al. 2022). However, seasonal behavioural plasticity is also possible, as observed for the European hare in Turkey between the cold and warm

seasons (Naderi et al. 2021). Indeed, activity patterns may vary across seasons in response to changes in abundance of trophic resources, mating behaviour, or adaptations to the behaviour of competitors and predators (Connolly et al. 2024; Vermeulen et al. 2024; Peris et al. 2025; Pixão et al. 2025).

Taking advantage of a long-term camera trapping (2012–2023) conducted in a restricted area (96 ha) of northern Italy, we analysed the full-year and seasonal diel activity patterns of the European hare, Eastern cottontail, and their main predator in the area, namely the red fox, before and after the colonisation of the alien Eastern cottontail in the area.

We hypothesise that:

H1) As a newly arrived species in an area where spatial segregation may be constrained by limited spatial extent, the Eastern cottontail has adapted its diel activity rhythm to reduce temporal overlap with the European hare, a potential competitor expected to dominate the Eastern cottontail because of its larger body size (see Mori et al. 2025a, b). H2) Following the arrival of the Eastern cottontail, the red fox has partially adjusted its diel activity rhythm to increase its chances of preying on the cottontail, which represents a suitable prey for this canid (Balestrieri et al. 2005; Cerri et al. 2017). H3) The European hare, expected to outcompete the Eastern cottontail, has not significantly altered its diel activity rhythm, except for finer modulations in response to potential changes in the red fox activity, which may track the rhythm of the Eastern cottontail if H2 is supported (Cerri et al. 2017).

Based on these hypotheses, we predicted that:

i) if H1 is supported, the observed activity overlap between the Eastern cottontail and the European hare would be significantly lower than expected by chance, with peaks (if any) either slightly shifted or occurring at different times;
ii) if H2 is supported, the observed activity overlap of the red fox would differ significantly from that expected by chance between the pre- to post-colonisation periods, partially tracking the activity of the Eastern cottontail;
iii) if H3 is supported following H1, the observed activity overlap of the European hare would not differ significantly from that expected by chance between the pre- and post-colonisation periods. Nevertheless, if H2 is also supported, finer adjustments, such as shifts in the activity peaks, may have occurred in the European hare to reduce temporal overlap with the red fox.

Materials and methods

Study area

The study was conducted in the Regional Natural Reserve "Le Bine", a protected area of 96 hectares in the Po Plain, located within a highly anthropised territory dominated by intensive arable cropping between the provinces of Cremona and Mantua (45.14° N, 10.44° E) (Fig. 1). Established in 1987, the reserve is part of the territory of the "Oglio Sud Regional Park" and is managed in collaboration with the World Wide Fund for Nature (WWF). In 2016, it was designated as Special Area of Protection under the Habitats Directive 92/42/EEC. The area originated from a meander cut of the Oglio River, leading to the formation of an oxbow lake. In the 1950s, the land was used for arable farming but was later converted to poplar plantations. Since the late 1980s, a series of interventions have been carried out to restore wetland areas and rewilding former agricultural lands. Beginning in 1994, poplar plantations were gradually cut and replaced with wetland vegetation and reforestations using native broadleaved tree species (Agapito Ludovici and Cecere 1996, 2003; Agapito Ludovici et al. 2012). Currently, the area is characterised by wetland vegetation, woodlands, clearings, and a small orchard. While the European hare and the red fox are historically present, the Eastern cottontail was detected for the first time in 2016 (https://www.lebine.it/mammiferi/).

Camera-trap survey

The camera-trap survey started in 2012 with a single sampling station being active (station H) as a qualitative investigation of the fauna in the protected area. Subsequently, in 2013, an extensive camera-trap survey was launched within the reserve to characterise the mammal community of the area, and it continued until 2023. Camera traps, equipped with passive infra-red motions sensor (Scout Guard® SG550-12 mHD, Scout Guard® SG2060-X, Scout Guard® BG962-30 W, Scout Guard® SG560K-18mHD, Bushnell® Nature View Cam HD), were deployed at 33 sampling locations to cover the full range of vegetation formations present within the study area over the study period (Table S1 in the Supplementary Information). Cameras were secured to trees at approximately 50 cm above ground level. They were neither baited nor placed at sites expected to have high animal traffic (trails or obligated passing points). Cameras were set to record 30-second videoclips continuously over the 24-hour period, with no time lapse between consecutive detections. To maximise resource availability and ensure sampling coverage, seven sampling stations were maintained over multiple years and were active for extended periods (range:

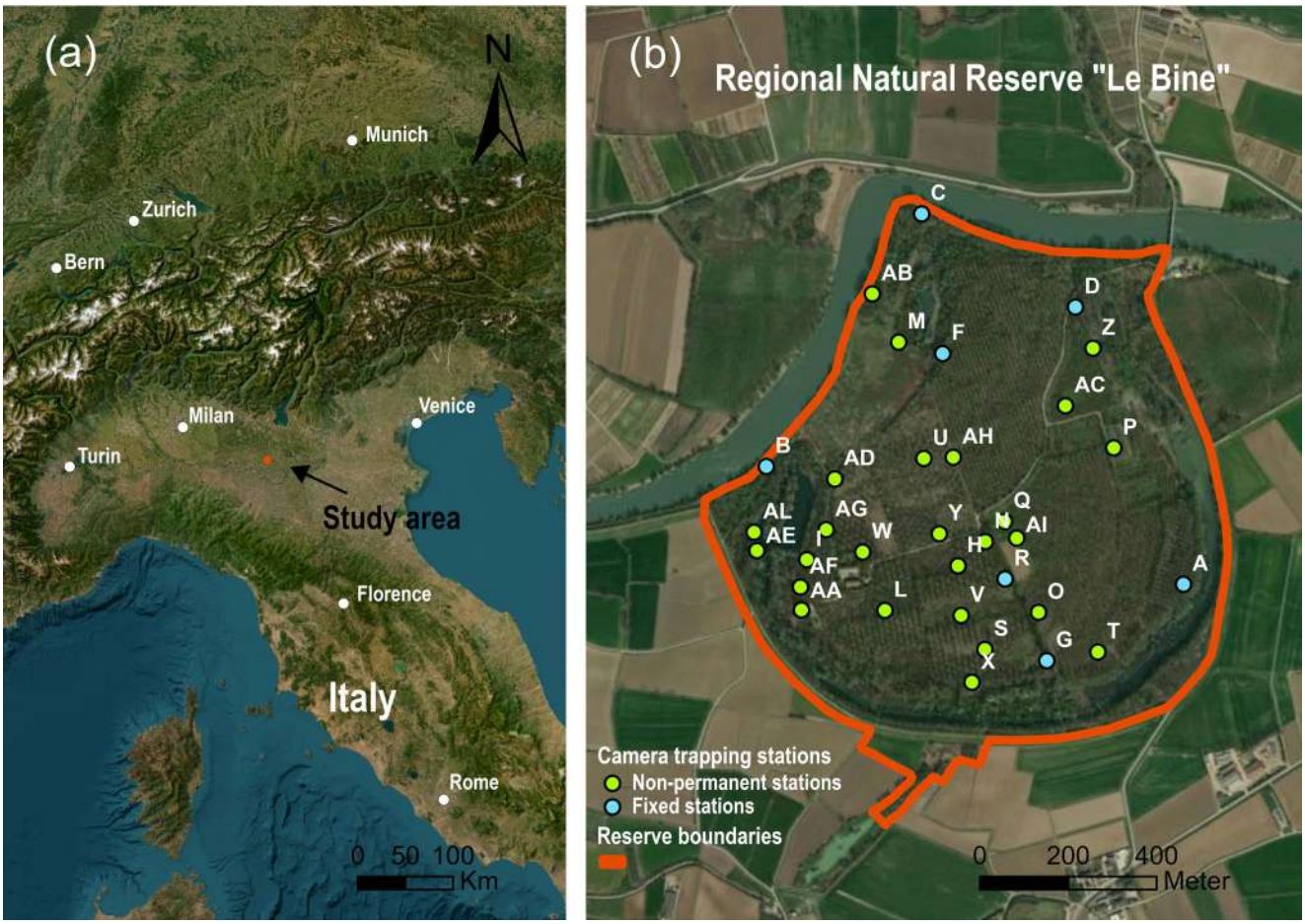


Fig. 1 Study area and sampling stations. In (**a**), location of the Regional Natural Reserve "Le Bine" in Italy; in (**b**), focused section on the study area with displacement of camera-trap stations

109–1,986 trap nights) both within and across years (fixed stations), whereas 26 stations were active for shorter periods (2–243 trap nights), with no or limited repetition across years (non-permanent stations) (Fig. 1b).

Data processing and survey periods

Considering the nature of the sampling scheme, which did not follow a standardised protocol, multiple procedures was applied to limit potential spatiotemporal autocorrelations. Consecutive detections of the same species from a camera trap were assumed temporally independent if recorded more than 15 min apart. This threshold was selected to avoid repeated detections of the same individual (e.g. individuals foraging around the camera trap) within short time intervals, while minimising the potential introduction of bias due to unjustified time-to-independence filtering (Peral et al. 2022; Smith 2024; Barnes et al. 2025). Camera traps that were located less than 100 m apart and active during the same period were not considered spatially independent; therefore, for these camera traps, data from the camera trap with the shortest operational period were removed from the analyses (i.e. 37 trap nights from three sampling stations in 2013, 2014, 2020). The year 2012 was excluded from the analyses as only one sampling station was active during this time.

The Eastern cottontail was first detected in the area in February 2016. However, between that initial sighting and the end of 2019, only 14 independent detections were recorded. Conversely, starting in 2020, the number of detections increased, with 100 recorded in that year alone. Therefore, we defined the period 2013–2019 as the pre-colonisation period, while 2020–2023 as the post-colonisation period. We assessed temporal segregation over the full year, as well as separately for the warm (May-August) and cold (November-February) 4-month periods, excluding transitional months to avoid temporal continuity between the two periods (see also Vidus-Rosin et al. 2012 and Mori et al. 2020 for similar approaches). Each of these three seasonal groupings were analysed separately for the pre- and post-colonisation phases, resulting in a total of six temporal windows.

Activity pattern analysis

All the analyses were implemented using R v. 4.3.2 (R Core Team 2023).

Time data were transformed into radians (0, 2π) and standardised relative to sunrise and sunset to account for variation in photoperiod across the year (Beasley et al. 2023). We applied a double-anchoring transformation that anchored activity time to the average sunrise and sunset across the study period (Vazquez et al. 2019) using the function *solartime* in the R package *activity* (Rowcliffe et al. 2014; Rowcliffe 2023). To represent sunrise and sunset times in the activity rhythms plots, we calculated the mean sunrise and sunset times across all days of each temporal window of the study period (full year, warm season, cold season) for the study area, using the function *get_suntimes* in the R package *activity*. Diel activity patterns were then estimated using the function *fitact* in the R package *activity*, through a non-parametric approach based on the Von Mises circular kernel density function (Ridout and Linkie 2009), with bandwidth calculated internally from the data. Confidence intervals (95%) of the estimated kernel functions were computed through a non-parametric bootstrap procedure (1,000 simulations). To quantify the overlap between activity patterns for each pair of density functions, we calculated the $\widehat{\Delta}_4$ estimator (hereafter overlap coefficient), which measures the overlap between two density functions (Schmid and Schmidt 2006; Ridout and Linkie 2009), using the function *ovl4* in the R package *activity*. This coefficient ranges from 0 (no overlap) to 1 (perfect overlap) and is appropriate when the number of observations of the smallest sample is ≥75 (Ridout and Linkie 2009; Meredith et al. 2024). The 95% confidence intervals for the overlap coefficient were obtained through a smoothed bootstrap procedure with 1,000 simulations using the functions *bootstrap* and *bootCI* in the R package *overlap* (Meredith et al. 2024). As the overlap coefficient is descriptive, we performed a randomisation test to statistically assess the overlap between a pair of density functions and evaluate the probability that two sets of circular observations originate from the same distribution. This test, performed using the function *compareCkern* in the R package *activity*, generated a null distribution of overlap coefficients by randomly resampling the data with replacement; the observed overlap coefficient was then compared with those generated from the null distribution to obtain statistical inference. Lastly, for each pair of activity patterns, we compared the daily activity levels through the Wald test (chi-square distribution on one degree of freedom) using the function *compareAct* in the R package *activity*. The daily activity level measures the proportion of time active (range = 0–1), which was calculated by dividing the area under the curve of the density function by the area within the rectangle bounded by the maximum of the curve and zero (Rowcliffe et al. 2014). It may be considered as a proxy of the usage of the available time.

Results

The total sampling effort amounted to 7,254 trap-nights across 33 distinct sampling locations, with 2,897 trap-nights and 23 sampling stations in the pre-colonisation period (2013–2019), and 4,357 trap-nights and 21 sampling stations in the post-colonisation period (2020–2023) (Table S2 in the Supplementary Information). The European hare was detected in 1,292 records (729 during the pre-colonisation period, of which 184 detections were observed in the warm season and 301 in the cold season; 563 during the post-colonisation period, of which 109 were observed in the warm season and 192 in the cold season), the red fox in 1,921 records (552 during the pre-colonisation period, of which 212 were observed in the warm season and 202 in the cold season; 1,369 during the post-colonisation period, of which 519 were observed in the warm season and 435 in the cold season), and the Eastern cottontail in 1,701 records (excluding the 14 record in the pre-colonisation period that were not used for the analyses), of which 359 were observed in the warm season and 654 in cold season.

Daily activity level

The red fox showed higher activity levels than both lagomorphs during the warm season (red fox: $0.453_{[pre]}$, $0.523_{[post]}$; European hare: $0.284_{[pre]}$, $0.248_{[post]}$; Eastern cottontail: $0.257_{[post]}$), and also higher activity than the Eastern cottontail during the cold season; conversely, the activity level between the European hare and the Eastern cottontail did not differ except for the full year (Table S3 and S4 in the Supplementary Information). For the red fox, the daily activity level did not differ between the warm and the cold seasons ($p > 0.05$) and was consistent between pre- and post-colonisation periods. Conversely, the two lagomorphs showed a higher daily activity level during the cold season than the warm season ($p \leq 0.05$), and for the European hare this pattern was consistent before and after the arrival of the Eastern cottontail (Table S3 and S4).

Diel activity patterns

Pre-colonisation species comparison

Before the arrival of the Eastern cottontail, the comparison between the European hare and the red fox showed a low degree of temporal overlap, especially in the warm season

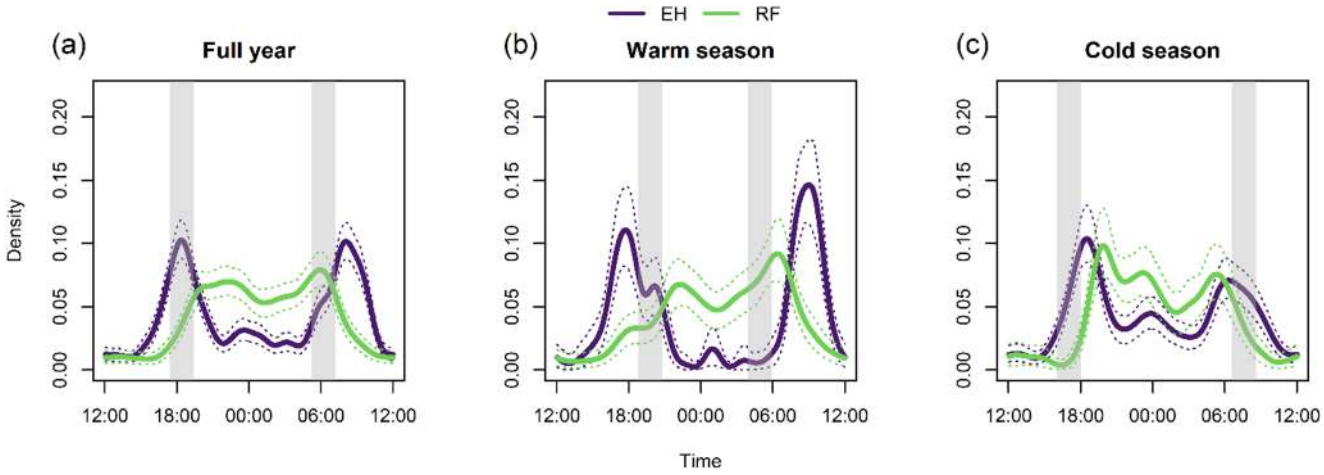


Fig. 2 Comparisons of full-year and seasonal activity patterns between the red fox and the European hare during the pre-colonisation period. Solid and dashed lines indicate the estimated activity and the corresponding bootstrapped 95% confidence interval, respectively. Vertical grey shaded areas represent the two-hour intervals spanning one hour before and after sunrise and sunset. EH = European hare; RF = red fox

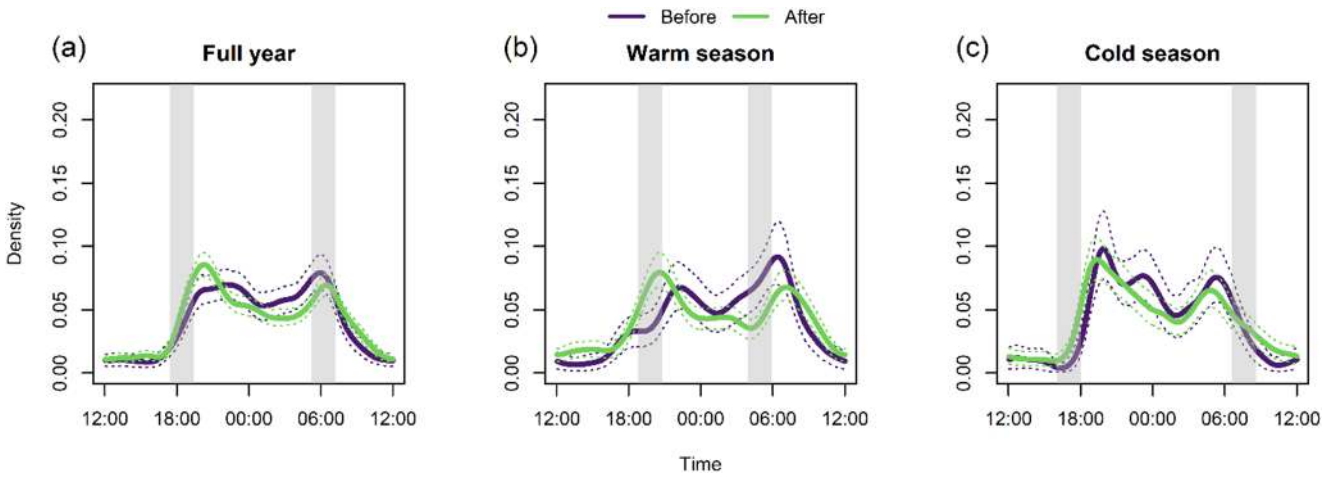


Fig. 3 Full-year and seasonal activity patterns of the red fox in relation to the colonisation of the Eastern cottontail. Before: pre-colonisation (2013–2019), after: post-colonisation (2020–2023). Solid and dashed lines indicate the estimated activity and the corresponding bootstrapped 95% confidence interval, respectively. Vertical grey shaded areas represent the two-hours intervals spanning one hour before and after sunrise and sunset

(overlap coefficient$_{[\text{full year}]}$ = 0.619 [95% CI = 0.552–0.645]; overlap coefficient$_{[\text{warm}]}$ = 0.431 [95% CI = 0.315–0.455]; overlap coefficient$_{[\text{cold}]}$ = 0.703 [95% CI = 0.606–0.749]; Fig. 2). Randomisation tests for the overlap coefficient showed that these patterns were different ($p < 0.001$ in all cases) (Table S4).

Red fox

The red fox showed nocturnal activity across both the warm and cold seasons as well as during the full year, with moderate peaks shifted toward the sunrise and the sunset (Fig. 3).

Despite the high temporal overlap before and after the colonisation of the Eastern cottontail in the area (overlap coefficient$_{[\text{full year}]}$ = 0.893 [95% CI = 0.857–0.933]; overlap coefficient$_{[\text{warm}]}$ = 0.822 [95% CI = 0.748–0.870]; overlap coefficient$_{[\text{cold}]}$ = 0.894 [95% CI = 0.860–0.966]), statistical difference emerged for the full-year and the warm season patterns ($p < 0.001$; Table S4). In the full year, a slight shift of the activity peak towards sunset was observed. In the warm season, both peaks shifted towards early morning and sunset, with a reduction in nocturnal activity. These detectable changes in the red fox's activity rhythms, associated with shifts in activity peaks, suggested that the red fox could have partially tracked the activity of the Eastern cottontail (see also the section "Post-colonisation species comparison"), thereby supporting our hypothesis H2.

European hare

The diel activity pattern of the European hare was strongly bimodal. Two peaks of similar intensity occurred approximately at, or immediately before or after, sunrise and sunset during the full year and the cold season; conversely, in the warm season a higher peak occurred in the morning, around four hours after the sunrise (Fig. 4).

Interestingly, this pattern was consistent both before and after the arrival of the Eastern cottontail, showing a high degree of overlap between the two periods (pre- and post-colonisation) across the full year and during both the warm and cold seasons (overlap coefficient$_{[\text{full year}]}$ = 0.913 [95% CI = 0.885–0.952], p = 0.089; overlap coefficient$_{[\text{warm}]}$ = 0.880 [95% CI = 0.853–0.999], p = 0.584; overlap coefficient$_{[\text{cold}]}$ = 0.915 [95% CI = 0.891–1], p = 0.578) (Table S4). This provided strong support for our hypothesis H3, in which the European hare did not modify its diel activity rhythm after the arrival of the Eastern cottontail.

Eastern cottontail

The Eastern cottontail showed a more plastic diel activity rhythm. Both full-year and cold season patterns were quite similar, with most of the activity spent during nocturnal hours and a crescent activity shifted toward the sunrise. Conversely, in the warm season, the species showed a strong peak in the morning, around three hours after the sunrise, while nocturnal activity was extremely reduced (Fig. 5).

Post-colonisation species comparison

In the post-colonisation phase, pairwise comparisons among all species were statistically significant (p < 0.001), supporting distinct diel activity patterns.

By comparing the temporal activity between the Eastern cottontail and the European hare, the overlap was moderate or relatively low. The overlap was higher in the warm season (overlap coefficient$_{[\text{warm}]}$ = 0.739 [95% CI = 0.652–0.812]), lower in the cold season (overlap coefficient$_{[\text{cold}]}$ = 0.560 [95% CI = 0.463–0.603], and intermediate across the full year (overlap coefficient$_{[\text{full year}]}$ = 0.690 [95% CI = 0.633–0.717]). In the warm season, when the overlap was higher, the peak of activity was shifted by one hour (at 8:00 a.m. and 9:00 a.m. for the Eastern cottontail and the European hare, respectively; Fig. 5). These results provided support for our hypothesis H1, in which the Eastern cottontail adapted its diel activity rhythm in response to the pre-existing presence of the European hare.

The temporal overlap between the Eastern cottontail and the red fox was higher during the full year (overlap coefficient$_{[\text{full year}]}$ = 0.881 [95% CI = 844–0.904]), lower in the warm season (overlap coefficient$_{[\text{warm}]}$ = 0.664 [95% CI = 0.596–0.712]), and with intermediate value in the cold season (overlap coefficient$_{[\text{cold}]}$ = 0.748 [95% CI = 0.694–0.792]). Notably, the red fox appeared to track the activity of the Eastern cottontail, adjusting its activity peaks to align with those of the lagomorph. Even when overlap coefficient was lower, as in the warm season, the red fox still reduced the temporal discrepancy in activity peaks by shifting them closer to those of the Eastern cottontail (Figs. 3b and 5). In this season, the red fox shifted its peaks from 22:16 (pre-colonisation) to 20:35 (post-colonisation), and from 06:23 (pre-colonisation) to 07:04 (post-colonisation), with

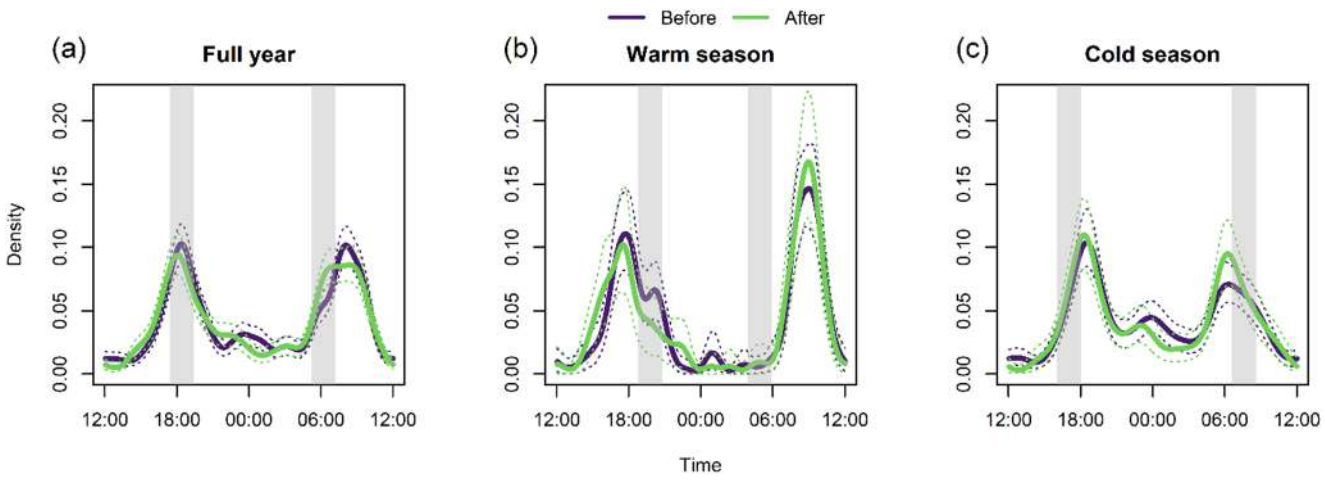


Fig. 4 Full-year and seasonal activity patterns of the European hare in relation to the colonisation of the Eastern cottontail. Before: pre-colonisation (2013–2019), after: post-colonisation (2020–2023). Solid and dashed lines indicate the estimated activity and the corresponding bootstrapped 95% confidence interval, respectively. Vertical grey shaded areas represent the two-hour intervals spanning one hour before and after sunrise and sunset

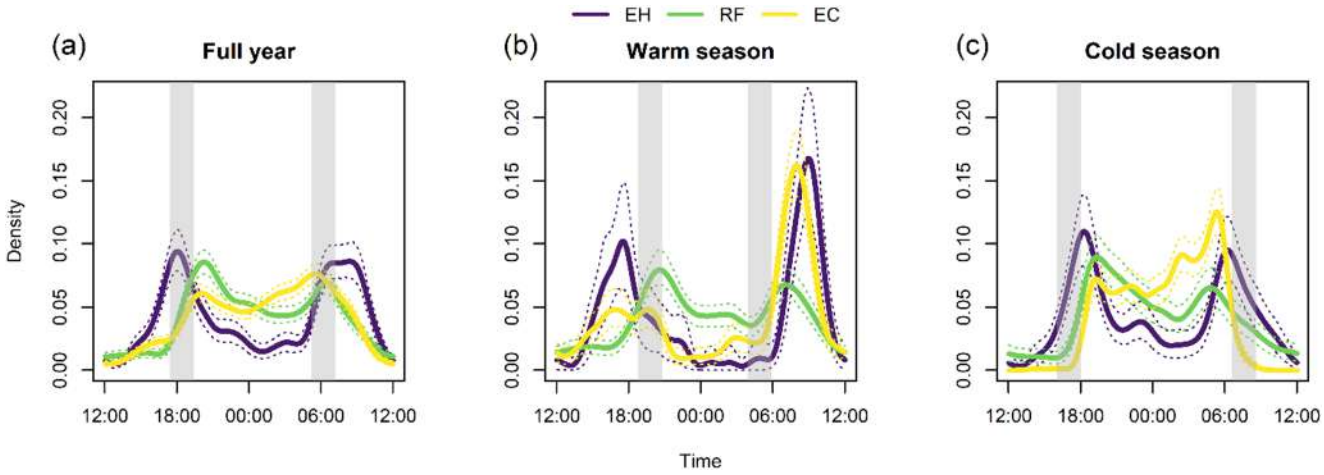


Fig. 5 Comparisons of full-year and seasonal activity patterns between the European hare, the red fox, and the Eastern cottontail during the post-colonisation period. Solid and dashed lines indicate the estimated activity and the corresponding bootstrapped 95% confidence interval, respectively. Vertical grey shaded areas represent the two-hour intervals spanning one hour before and after sunrise and sunset. EH = European hare; RF = red fox, EC = Eastern cottontail

a reduction in nocturnal activity. This pattern appeared to track the reduced nocturnal activity of the Eastern cottontail, which exhibited peaks in the late afternoon and especially early morning.

The temporal overlap between the European hare and the red fox were consistent between pre- and post-colonisation period (full year: $0.619_{[pre]}$ and $0.689_{[post]}$; warm season: $0.431_{[pre]}$ and $0.519_{[post]}$; cold season: $0.703_{[pre]}$ and $0.718_{[post]}$; Table S4). Moreover, no subtle changes in the activity of the European hare (e.g. shifts in activity peaks) were observed. Given the low-to-moderate activity overlap between the European hare and the Eastern cottontail, the observed temporal tracking of the Eastern cottontail's activity rhythm by the red fox (hypothesis H2) did not significantly affect the European hare' activity rhythms.

Discussion

This research represents the first long-term assessment of temporal partitioning among two lagomorphs, the native European hare and the alien Eastern cottontail, and their main predator in the study area, the red fox, before and after the colonisation of the territory by the Eastern cottontail.

The comparison of the diel activity rhythms between the European hare and the red fox highlighted different activity patterns and showed a low degree of temporal overlap that remain consistent after the Eastern cottontail's colonisation. The red fox showed mainly nocturnal and crepuscular activity, in agreement with previous studies on this species (Cavallini and Lovari 1994; Monterroso et al. 2014; Díaz-Ruiz et al. 2016; Torretta et al. 2017, 2021). In contrast, the European hare showed very low nocturnal activity. Although this lagomorph was often reported as a primarily nocturnal species (Zaccaroni et al. 2013; Viviano et al. 2021; Mori et al. 2022), it could exhibit behavioural plasticity depending on local conditions (Holley 2001; Naderi et al. 2021). For example, during summer, when the nights are probably too short to allow individuals to cover their energetic requirements, hares were reported to have activity peaks in full daylight (Schai-Braun et al. 2012). In our study area, the European hare showed a strong bimodal activity patterns with two peaks around sunrise (or early morning) and sunset, which remained unchanged before and after the cottontail's colonisation, even when seasonality was considered. In a restricted area like this, temporal partitioning could represent an important mechanism for reducing predation risk (Chen et al. 2025). Our findings suggested that temporal segregation could serve for reducing encounters with the red fox. However, the red fox is a generalist and opportunistic predator (Soe et al. 2017). In the absence of specific information on its diet in the study area, we could not exclude that the canid's food habits might be more oriented towards other sources rather than the European hare, resulting in limited temporal overlap with the lagomorph, as it did not markedly track the hare's activity.

The Eastern cottontail emerged as a behaviourally plastic species. In its native areas, this species is mainly nocturnal (Andrade-Ponce et al. 2022; Palomo-Munoz et al. 2024). In our invaded area, its diel activity patterns varied seasonally: while nocturnal in the cold season and over the full year, the species shifted to a bimodal pattern in the warm months, marked by a prominent peak in the early morning (three hours after sunrise) and a reduced level of nocturnal activity. This behavioural flexibility enforced previous findings highlighting the plasticity of daytime usage that the

species can adopt in invaded ranges (Panzeri et al. 2021). The diel activity of the Eastern cottontail showed moderate to low overlap with the European hare, especially in the cold season, and a higher overlap with red fox. These findings suggested that the alien Eastern cottontail adapted its diel activity patterns in relation to its competitor, the European hare, and its main predator, the red fox. Particularly, the alien lagomorph appeared to be more oriented to reduce encounters with the hare rather than lowering the risk of predation by red fox. Temporal partitioning may be particularly pronounced under sympatric conditions (Gálvez et al. 2021), especially when populations occur in size-limited areas, where spatial avoidance of competitors and predators may be more difficult to adopt as a behavioural response. Indeed, when key resources (e.g. food) are less limiting, such as in the warm season, the temporal partitioning between the two lagomorph species is lower, although a subtle modulation was observed in a one-hour offset between the peak activity of the cottontail (8:00 a.m.) and that of the European hare (9:00 a.m.). This modulation may represent an adaptive form of temporal partitioning that reduces interference competition. Accordingly, the lower daily activity level (proxy of the use of the available time) observed in the warm season for both lagomorph species could reflect a higher food availability in late spring and summer, which could reduce the time required for foraging. However, potential increases in human disturbance during the warm season may further constrain the temporal activity of the two herbivores' species, prompting individuals to limit activity to avoid potential encounters with humans (Mori et al. 2025a). Conversely, during the cold season, resources may be scarcer, forcing individuals to occupy the same fine-scale spatial locations and spend more time foraging, as suggested by their higher daily activity levels. Under these conditions, coexistence between the Eastern cottontail and its competitor, the hare, may be strongly promoted through temporal segregation.

Despite the high overlap in red fox activity patterns and the consistency of its daily activity level between the pre- and post-colonisation periods, the species showed subtle yet statistically significant adjustments in its warm season and full-year patterns following the cottontail colonisation. Such shifts might indicate an adaptive realignment of foraging strategies in response to shifting prey availability or interspecific encounters (Cerri et al. 2017), in line with the generalist and opportunistic nature of this predator. By remaining active for approximately half of the daily period, the red fox could maximise foraging opportunities in relation to food availability and local environmental conditions.

The temporal overlap between the European hare and the red fox remained largely unchanged by the cottontail's colonisation, suggesting that the existing predator–prey temporal dynamics were not markedly modified by the colonisation of the alien Eastern cottontail. We suggested that the red fox refined its diel activity patterns to track those of the Eastern cottontail, increasing the possibility of encounters with this novel prey. However, since the observed activity patterns of the Eastern cottontail differed from those of the European hare (but see Mori et al. 2025a for urban areas), these adjustments did not significantly affect the European hare's activity rhythm, which was therefore unlikely to be exposed to an increased risk of predation by the red fox.

To summarise, temporal segregation emerged as a supported mechanism to promote coexistence between the two lagomorphs, with temporal dynamics further modulated by seasonal conditions. The long-term stability of the diel activity rhythm of the European hare suggested that the species was resistant to potential competitive pressures from the alien Eastern cottontail. The behavioural plasticity of the Eastern cottontail in adapting its diel activity rhythm to reduce overlap with the European hare could represent a key mechanism underlying its establishment in invaded ranges (see also Sogliani et al. 2025; for potential competition between Eastern cottontail and European rabbits *Oryctolagus cuniculus*, in a nearby study area). The red fox also appeared to partially track the activity pattern of the alien lagomorph. Consequently, any putative cascading effects on the European hare's activity rhythms may depend on the degree of overlap between this temporal tracking and the hare's own activity pattern. Although temporal segregation can promote species coexistence, in the absence of demographic estimates we cannot determine how the arrival of the alien lagomorph could affect population-level responses or whether this mechanism provides an adaptive advantage to one or both lagomorphs in the long term. Additionally, we stress that, even under sympatric conditions within size-limited areas, spatial segregation could represent an important mechanism interacting with temporal partitioning in shaping interspecific dynamics and coexistence among species, particularly when fine-scale habitat selection or spatial avoidance is possible, as in the case for the European hare and the Eastern cottontail. Future studies should aim to disentangle the underlying drivers of spatial and temporal patterns in sympatry. Factors such as habitat structure, resource availability, and direct/indirect interspecific interactions (e.g. competition and predation) are crucial for a deeper understanding of coexistence mechanisms between native and alien species. Finally, linking these mechanisms with demographic estimates would be pivotal for scaling up responses at population level and developing effective conservation and management strategies.

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Data availability The data that supports the findings of this study will be available from the corresponding author upon reasonable request.

Declarations

Ethical approval Not applicable.

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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