Applied Animal Behaviour Science 284 (2025) 106534

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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

# What a camera trap survey can reveal about the behaviour of an invasive species: Insights from coypus *Myocastor coypus* in an urban park of central Italy

Andrea Viviano [a,1], Leonardo Ancillotto [a,b,2,*], Olivia Dondina [b,c,3], Alice Burchielli [d], Daniela Miccolis [e], Emiliano Mori [a,b,4]

[a] *Istituto di Ricerca sugli Ecosistemi Terrestri IRET, Consiglio Nazionale delle Ricerche, Via Madonna del Piano 10, Sesto Fiorentino, Florence 50019, Italy*
[b] *National Biodiversity Future Center, Palermo 90133, Italy*
[c] *Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 1, Milano 20126, Italy*
[d] *Department of Biology, University of Pisa, Via Alessandro Volta 4 bis, Pisa 56126, Italy*
[e] *Environments Service, Municipal Council of Empoli, Via Giuseppe del Papa 41, Empoli, Firenze 50053, Italy*

ARTICLE INFO

*Keywords:*
Activity rhythm
Ethogram
Invasive alien species
Rodentia
Wildlife management

ABSTRACT

Assessing the behaviour of invasive alien species is fundamental for their management. Coypu occurrence outside the native range poses ecological and economic threats, and effective management strategies are crucial, particularly in urban areas where interactions with humans are the most frequent. In this work, we analysed the temporal patterns of activity and behavioural repertoire of an urban population of coypus in central Italy, by means of camera trapping and focal sampling. Activity rhythms and time budget were estimated throughout the year and compared across seasons, sexes, and age classes; overlaps in coypu activity patterns with co-occurring potential predators and competitors were also assessed. Differently from natural areas, coypus in our study site were primarily crepuscular and nocturnal, with a significant reduction in activity during bright moonlight periods to limit predation risk, showing a high overlap with red foxes (the main natural predator) but minimal overlap with humans and unleashed dogs. Coypus spent most of their time swimming and foraging. Adult males were territorial and were the only sex scent-marking on both land and woods. Adult females played a crucial role in protecting offspring, together with subadults, and defended dens with cubs from conspecific and other species. Playing was strictly a kit prerogative. In general, controlling coypu populations, as imposed by EU regulations, is challenging due to their adaptability and high reproductive rate. We suggest that trapping efforts should focus on night-time activities near water bodies during warmer months, when coypu are more active on the land and thus more likely to encounter land-based traps. Overall, this study provides valuable insights into the ecology and behaviour of coypu in urban environments, aiding in the development of effective management strategies to mitigate the species impacts on native biodiversity and environments.

## 1. Introduction

Invasive alien species are a major driver of biodiversity loss, causing local extinctions and increasing the number of species classified under threat categories by the International Union for Conservation of Nature (IUCN) (Pyšek and Richardson, 2010). These species are brought to attention by the EU Regulation 1143/2014, which includes a black-list of highly-invasive species of conservation concern, together with guidelines for their management, ratified by individual countries (Carboneras et al., 2018).

* Corresponding author at: Istituto di Ricerca sugli Ecosistemi Terrestri IRET, Consiglio Nazionale delle Ricerche, Via Madonna del Piano 10, Sesto Fiorentino, Florence 50019, Italy.

*E-mail addresses:* andrea.viviano@iret.cnr.it (A. Viviano), leonardo.ancillotto@cnr.it (L. Ancillotto), emiliano.mori@cnr.it (E. Mori).

[1] 0000–0002-2970–3389
[2] 0000–0002-8774–0671
[3] 0000–0001-8097–1971
[4] 0000–0001-8108–7950

https://doi.org/10.1016/j.applanim.2025.106534
Received 7 November 2024; Received in revised form 24 January 2025; Accepted 30 January 2025
Available online 31 January 2025

Among black-listed taxa, the coypu *Myocastor coypus* (Rodentia, Myocastoridae), a large semi-aquatic rodent native to South America, has become widespread in Europe (Carter and Leonard, 2002). The coypu expanded in Europe due to initial releases for fur farming and subsequent escapes, aided by their high reproductive rate and adaptability to diverse environments, including human-modified landscapes (Schertler et al., 2020). Currently, the coypu is widely distributed, ranging longitudinally from Spain, near the French border, to Ukraine, and latitudinally from Greece to Denmark and Lithuania (Bertolino and Genovesi, 2007; Schertler et al., 2020). In Italy, coypus were first introduced in 1928 at the National Rabbit Breeding Institute in Alessandria, Piedmont (North-Western Italy) and currently occur throughout the Peninsula and the main islands (Cocchi and Riga, 2001; Bertolino and Cocchi, 2018); the species largely occurs in both urban and more natural areas (Bertolino and Cocchi, 2018; Ancillotto et al., 2024). Studies on coypu management and distribution have been conducted in Argentina (native range), and several European countries (Doncaster and Micol, 1989; Reggiani et al., 1995; Poláčková et al., 2022; Salas et al., 2022). Great Britain is the only country where an eradication project has been successfully implemented (Baker, 2006; Kil et al., 2015). By contrast, in most European countries, including Italy, the species has considerably expanded despite multiple numerical control actions, because long-term eradication campaigns have never been concluded (Bertolino and Cocchi, 2018).

The coypu negatively impacts native species, such as the Eurasian beaver *Castor fiber* and water voles *Arvicola* spp., through direct competition for space and resources (e.g., dens: Ruys et al., 2011; Ladent et al., 2022), although current evidence is still weak. Moreover, habitat alterations and the transmission of potentially zoonotic diseases are major causes of ecological imbalance, posing a significant threat to public health, infrastructures, and native wildlife conservation (Corriale et al., 2006; D'Adamo et al., 2000; Bertolino et al., 2005, 2011; Dondina et al., 2024). This underscores the need for effective and sustainable management of this species, particularly in urban environments, where potential interactions with humans are at their highest (Bertolino and Cocchi, 2018).

Knowledge on time budget and activity patterns may help in designing effective management strategies informed by animal ecology (McLeod et al., 2015; Dell'Agnello et al., 2020). Coypu behaviour is still very poorly known. Some behavioural patterns have been studied in captive animals (Gosling, 1979), while observations in the wild are mostly restricted to dietary preferences and social structure (Guichón et al., 2003a, 2003b). Behavioural observations conducted in enclosures are inherently limited, as captive animals often exhibit an altered or reduced behavioural repertoire (e.g., Hosey, 2005; Mason et al., 2013; Lovari et al., 2020).

Regarding the behaviour of coypu under natural conditions, few studies have been conducted on resource use, behavioural and activity patterns (Amori et al., 2008). Interactions between coypu and humans in urban environments are particularly delicate and poorly investigated (Viviano et al., 2024). In urban areas of Argentina, coypus maintain primarily nocturnal and crepuscular activity patterns, with seasonal variations (Salas et al., 2022). Their activity extends into twilight more than observed in their natural habitat, suggesting reduced perceived danger in urban settings. In urban areas across the introduced range, Meyer et al. (2005) noted that artificial feeding along a river altered the activity patterns of the resident coypu population, bringing this species to be more diurnal. Mori et al. (2020a) compared activity rhythms in peri-urban and natural areas in central Italy, confirming that urban coypus are more active at night and twilight, whereas being predominantly diurnal in natural areas. Despite the well-documented presence of coypu in many Italian cities (Viviano et al., 2024), studies evaluating the behaviour of this species in urban areas are still lacking. Investigations into invasive alien species are particularly critical in regions where interactions with human activities are most frequent and where the risk of zoonotic disease transmission is elevated, i.e. in urban parks. Our study aimed at examining the behaviour of coypu in an urban environment of central Italy. The primary objectives were to describe the behavioural repertoire observed, and to estimate the temporal distribution of activities throughout the day and throughout the year. This research is an integral component of a broader initiative on urban biodiversity management (NRRP, National Biodiversity Future Center, Spoke 5), which is a primary concern of both national and European policies. The overarching goal was to elucidate species dynamics and enhance management strategies for alien species in urban areas. In particular, we predicted that: *i)* urban coypu are well adapted to human presenceand urban ecosystems, exhibiting high levels of nocturnal activity due to low predator risk, even when compared with patterns of activity rhythms of humans and potential predators (red fox *Vulpes vulpes* and unleashed dogs *Canis familiaris*); *ii)* coypu behaviour in urban environments is more complex than previously described, with clearly distinguishable community dynamics; *iii)* small towns and urban parks may serve as important case study for conducting ethological studies, thereby focusing attention on local wildlife and fostering community awareness and responsibility.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the urban park of Serravalle in the town of Empoli (province of Florence, Tuscany Region, Central Italy, 43.72°N 10.96°E). The park is 23 ha and hosts an artificial lake of 1.2 ha. About 39.0 % of the park was covered by meadows, 29.5 % by trees (*Pinus pinea* L., *Quercus ilex* L., *Quercus pubescens* Willd., *Populus nigra* L., *Arbutus unedo* L. and *Punica granatum* L.), 18 % by human settlements (also including a bar and a parking area) and 7.5 % by a maize (*Zea mays* L.) cultivation.

The site is characterised by an average temperature of 14°C, with the hottest months (July and August) with an average maximum temperature of 30°C and the coldest month (January) with an average minimum temperature of 1°C. Precipitation averages around 78 mm/month annually, with November being the wettest month (138 mm on average) and July the driest (an average of 31 mm of rain) (https://it.climate-data.org. Accessed on 01.11.2024).

Over the past few years, at least 10–15 coypu individuals have been observed in the park, adding to a diverse animal community primarily composed of several waterfowl and wader bird species, and the non-native American pond slider *Trachemys scripta* (Viviano et al., 2024). At the time of this study, about ten individual coypus were observed simultaneously (personal observation).

The presence of coypus was confirmed through direct observation (when they moved in the water or on land, emerging from their burrows) and presence signs such as droppings, footprints, slides on the banks, and near 30 burrow entrances (Viviano et al., 2024). By 2022, these signs of activity had spread around much of the lake perimeter, creating holes in the ground that can go unnoticed, particularly when vegetation is well-developed, posing a potential hazard for park visitors. This population became isolated from other coypu populations in the Tuscany Region following the excavation of the river dead arm in the area known as 'Arnovecchio', which rendered the area unsuitable for this rodent. Besides a general appreciation by the general public (Viviano et al., 2024), no complaint about coypu presence and activity has ever been received by the local municipal council.

### 2.2. Behavioural observations: camera trapping and focal sampling

Behavioural data were collected through camera trapping from May 2023 to April 2024, utilising infrared sensor camera traps (Browning® SpecOps model, Browning Trail Cameras, USA). This model features a high trigger speed (< 1 sec), which is crucial for minimising the risk of missing parts of the behavioural sequences exhibited by the animals captured on camera (O'Connell et al., 2011). Given the limited area occupied by coypus (approx. 0.10 ha), a single camera trap was used to avoid pseudo-replication due to capturing the same event on multiple devices simultaneously. The camera trap was strategically positioned to maximise the likelihood of detecting the target on both land and water, following an opportunistic sampling design (O'Connell et al., 2011). The camera was set to record 30 sec videos continuously, on a 24/7 schedule.

The chosen location was a section of the artificial lake shore characterised by numerous signs of coypu presence (den entrances, droppings and footprints). The camera trap was mounted on a pomegranate *Punica granatum* (L., 1753) branch, approximately 40–50 cm above the ground, oriented to capture both the shore with den entrances, and parts of the lake and surrounding land (Fig. S1 in Supplementary Material 1). It was kept active for one year, every day 24 h/24, and checked every 7–14 days, to download the recorded data and check the battery and memory card status.

Focal sampling sessions were also conducted to better identify different individuals also observed through camera trapping, by focusing on a single individual per session. These further behavioural observations were directly carried out by the authors between April 2023 and April 2024 in 20-min sessions, for one day per week and a total of 120 hours of recording. During each session, a visible subject at the start was observed for the entire duration of the session. Behavioural patterns were recorded in the order they were exhibited, and the duration of each behaviour was noted. This method provided information on the time spent on each activity, along with the observed behavioural patterns. Videos were analysed from two independent operators (EM and AB) after a common training.

Individuals were categorised into age classes based on body size, separating adults, subadults, and kits (Cosma, 2001; Amori et al., 2008). When age class could not be determined, individuals were classified as ND ("not determined"). Individual identification proved to be rather complex and was only possible for some individuals exhibiting truncated tails, scars, or differently coloured teeth. Sex was determined only in sexually mature individuals (characterised by a larger body size, estimated by eye) among those individually identified, through the observation of primary sexual characteristics (penis, testes) or evident nipples during the lactation season. When sex could not be determined, individuals were classified as ND (not determined).

### 2.3. Ethical and legal constraints

Camera trapping in the Serravalle urban park was conducted under a specific permit obtained from the municipality of Empoli. In accordance with agreements and in compliance with national and international privacy laws (Legislative Decree 196/2003 and European Regulation 2016/679), an informative panel was installed to inform park visitors about the presence of the camera trap, and to clarify the main aims of this research. The panel also included a QR code, which allowed visitors to download project documentation and provided assurance that any videos capturing humans would be immediately deleted from both the SD card and any other data storage systems. Additionally, it guaranteed the removal of all videos containing human subjects within 72 h of recording, and it facilitated immediate intervention by direct contact with the project manager (Supplementary Material 1).

### 2.4. Behavioural repertoire description

To describe the behavioural repertoire, we integrated patterns reported by Gosling (1979), for coypus); Bau (2001), for Eurasian beavers) and Poláčková et al. (2022), for coypus), including new patterns observed during the present study (Table S1 in Supplementary Material 1).

### 2.5. Patterns of activity rhythms

The dataset for estimating activity rhythms was compiled exclusively from camera trap video data. To limit bias from pseudo-replication, videos recorded within the same 30-minute interval were treated as a single independent event (Monterroso et al., 2014), retaining only the first video from the interval. The remaining videos were considered a random sample from a distribution describing the probability of a video being recorded at each specific time of day (Linkie and Ridout, 2011).

Statistical analyses were conducted using R version 4.1.1 (R Core Team, 2018), using the *dplyr* package (Wickham et al., 2014) for dataset manipulation and the *overlap* package (Meredith and Ridout, 2021) for estimating activity rhythms. The *overlap* package employs a kernel density estimation function to return the density of activity at each time of the day (Wand and Jones, 1994). The function uses a bandwidth parameter, k, which determines the resolution of the estimated curve; given this is an exploratory investigation (lacking prior knowledge about the species' activity distribution over the 24 h in the studied site), the parameter was set to its default value, $k = 1$ (Wand and Jones, 1994; Ridout and Linkie, 2009). Additionally, to test whether the observed activity over the 24 h significantly differed from uniformly distributed activity throughout the day, the Hermans-Rasson test (HR $r$ test: Landler et al., 2019) was applied using the *circMLE* package (Fitak and Johnsen, 2020).

We computed the Interseasonal overlaps of coypu activity rhythms. The Mardia–Watson–Wheeler test ($W$) was used to compare overlaps of circadian distribution of coypus amongst seasons (Massara et al., 2018), through the package *circular* (Lund et al., 2017). Furthermore, the overlap of coypu activity rhythms with those of co-present species was estimated. Potential predators of the coypu, such as the red fox *Vulpes vulpes* and the domestic dog *Canis familiaris* (Koynova et al., 2023; Sogliani et al., 2023), were considered, along with the overlap of coypu rhythms with human activity, although coypus are only occasionally preyed upon by these species (Reynolds, 1979; Koynova et al., 2023). To determine the overlap of activity rhythms between two species, the overlap coefficient $\Delta$ (ranging from 0, no overlap to 1, total overlap) was calculated using functions from the *overlap* package. Specifically, $\Delta_4$ was used since the number of records for all species exceeded 50 (Meredith and Ridout, 2021). Ninety-five percent confidence intervals (95 % CI) were calculated using 10,000 bootstrap replicates (Dias et al., 2019). Overlap was defined as intermediate with $\Delta$ between 0.50 and 0.75, high with $\Delta$ between 0.75 and 0.90, and very high with $\Delta > 0.90$ (Monterroso et al., 2014).

A chi-squared test was used to estimate whether records of coypus and red foxes (i.e., the only nocturnal predator occurring in Serravalle urban park) were uniformly distributed throughout all the four moon phases, classified as follows: phase 1: from new moon to ¼; phase 2: from ¼ to ½; phase 3: from ½ to ¾; phase 4: over ¾ (Mori et al., 2020).

### 2.6. Time budget and ethogram

We analysed the behaviour of coypu recorded in a dummy dataset using a binary approach (0 for non-observed, and 1 for observed) to indicate which behaviour was observed in each video for each coypu individual. The dataset was first cleaned to ensure that all categorical variables—'age class' (adult, subadult, kit), 'sex' (female and male, only for adult individuals), and 'season' (spring, summer, autumn, winter, following astronomical seasons)—were correctly encoded. Observations with missing values in 'sex' or 'age class' variables were excluded from the analysis.

To calculate the total amount of each behaviour across the year, we employed a standardised approach to determine the temporal distribution of behaviours. First, the total amount of time (in seconds) for each behaviour was calculated by selecting the relevant columns and transforming the data into a long format. In a long format, each row represents a single observation, with columns for the type of behaviour and its duration, making it easier to manipulate and analyse the data. Data were then filtered to include only observed behaviours (value = 1). Then, the total duration for each behaviour was summed.

After obtaining the total seconds for each behaviour as listed in the compiled ethogram (table S1 in Supplementary material 1), the overall sum of seconds was calculated to verify data accuracy. This sum was used as the total observed time, to normalise collected data. The activity budget for each behaviour was then expressed as a percentage of the total observed time, calculating the proportion of seconds dedicated to each behaviour with respect to the total.

We then analysed data by season, creating graphs and tables to visualise the activity budget for each season. Additionally, we inspected data by sex and age class, generating radar charts for each category.

We filtered the dataset to include only the relevant rows and columns for the chosen variable, then we calculated the total duration for each behaviour. Data were then transformed into a long format, and missing behaviours were accounted for by assigning them a value of 0. The activity budget for each behaviour was normalised as a percentage of the total observation time. A radar chart was generated to visualise the activity budget distribution.

We employed generalised linear models (GLMs) with a binomial error distribution to assess the influence of each categorical variable on the selected behavioural patterns (Zuur et al., 2007). Analyses were conducted with the R package *lme4* (Bates et al., 2015). Separate models were fitted for 'sex', 'age class', and 'season'. Our analysis focused on behaviours for which we had a substantial number of observations and which were hypothesised to vary across seasons, sexes, and age classes (see Gosling, 1979; Gosling and Wright, 1994), specifically: allogrooming, self-grooming, nose touching, parental care, vigilance, scent marking, and playing. These behaviours were chosen based on their expected variability in relation to the categorical variables, contrasting with behaviours like swimming, foraging, and exploring, which were not hypothesised to show significant variation (cf. Introduction). To identify key behaviour drivers, we evaluated the presence of significant effects of specific variable levels and used the adjusted $R^2$. Adjusted $R^2$ provides a more nuanced view of a model ability to explain variance in the response variable by adjusting for potential overestimation caused by additional predictors (James et al., 2021). For each model, we also developed a post-hoc test to inspect possible significant differences between all the levels of the considered categorical variable through the Tukey test using the *emmeans* (Lenth, 2024) R package.

## 3. Results

The cumulated sampling effort resulted in 351 camera-days. We collected a total of 2601 videos belonging to 30 species of mammals and birds (Fig. S1 in Supplementary Material 1). Amongst those, 1416 videos belonged to coypus. Potential predators/competitors of coypus included humans (238 videos), unleashed domestic dogs (96 videos) and red foxes (66 videos).

### 3.1. Activity rhythms

Annual temporal patterns of coypus significantly differed from random activities in the 24 hours cycle, peaking at dawn and dusk (HR test $r = 196.98$, $p < 0.01$: Fig. 1).

We detected a moderate-to-high seasonal overlap of coypu activity pattern, apart from winter, when activity was concentrated in early morning and late afternoon (Fig. 2a). Intraspecific seasonal overlaps did not significantly differ from one-another (Mardia Watson Wheeler tests, $W = 0.075$–$0.092$, all $p > 0.11$).

As to competitors and predators, we observed a low overlap with humans and unleashed dogs, whereas temporal overlap between red foxes and coypus was high (Fig. 2b).

In all seasons, the nocturnal activity of coypus was the lowest in bright moonlight nights ($\chi^2 = 12.93$–$21.22$, all $p < 0.05$), whereas that of the red fox was always independent to moon phases ($\chi^2 = 2.67$–$4.11$, $0.24 < p < 0.55$).

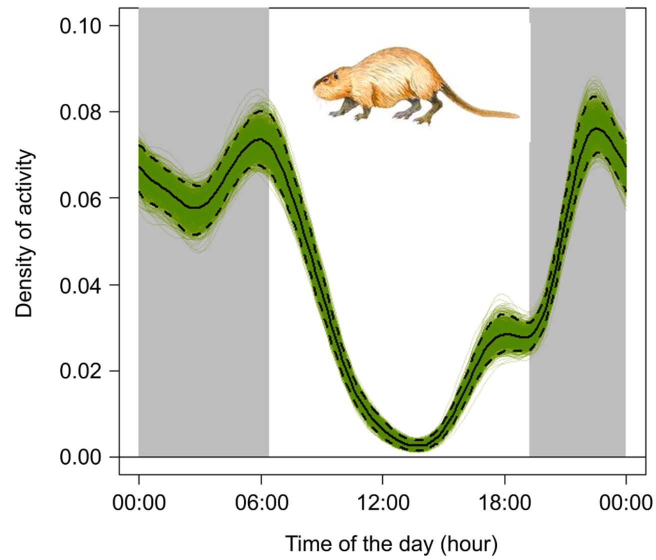


**Fig. 1.** Kernel density estimate of activity rhythms throughout the year of urban coypu in Serravalle urban park (solid line, mean). Green lines represent bootstrap estimates, and dashed black lines represent 95 % confidence intervals. Blue bands represent mean dark hours in the 24 h cycle.

### 3.2. Activity budget of coypu in urban environment

#### 3.2.1. Annual activity budget

Through camera trap video analysis, we determined that the annual activity budget of coypu, without distinguishing between age class, sex, or seasonality, reveals the following distribution of main activities: exploring (23.80 %), swimming (22.63 %) correlated with activity of entering/exiting water (1.54 %), self-grooming (15.64 %), and running (5.16 %). Their feeding habits are represented through various behaviour patterns, including foraging on natural food sources (11.85 %), feeding on food provided by park visitors (4.46 %), and eating in water (unidentified food: 3.15 %). Additional activities include vigilance (2.96 %), playing (2.60 %), and resting (2.46 %). Other patterns were observed at frequencies < 1.00 % (Fig. 3).

#### 3.2.2. Seasonal activity budget

Across the four seasons, without filtering for age class or sex, we observed different percentages of activities and behaviour (Fig. 4 and Table S1 in Supplementary Material 2). In spring, the predominant patterns were exploring and self-grooming, in summer exploring, in autumn exploring and swimming, and in winter swimming and self-grooming. Regarding social behaviour, which include those relevant to social interactions such as vigilance and aggressive behaviour, the following patterns were observed:

1) Playing: summer (6 %) > spring (3.6 %) > autumn (2.6 %) > winter (0.6 %)
2) Scent marking: winter (1.0 %) > autumn (0.7 %) > summer (0.4 %) > spring (0.0 %)
3) Vigilance: summer (6.8 %) > spring (3.2 %) > autumn (2.9 %) > winter (1.3 %)
4) Vocalisation: winter (0.3 %) > spring (0.1 %) > autumn (0.0 %) = summer (0.0 %)
5) Aggressive behaviour: summer (0.4 %) > winter (0.3 %) > spring (0.2 %) > autumn (0.0 %)
6) Allogrooming: winter (0.3 %) > spring (0.0 %) = summer (0.0 %) = autumn (0.0 %)

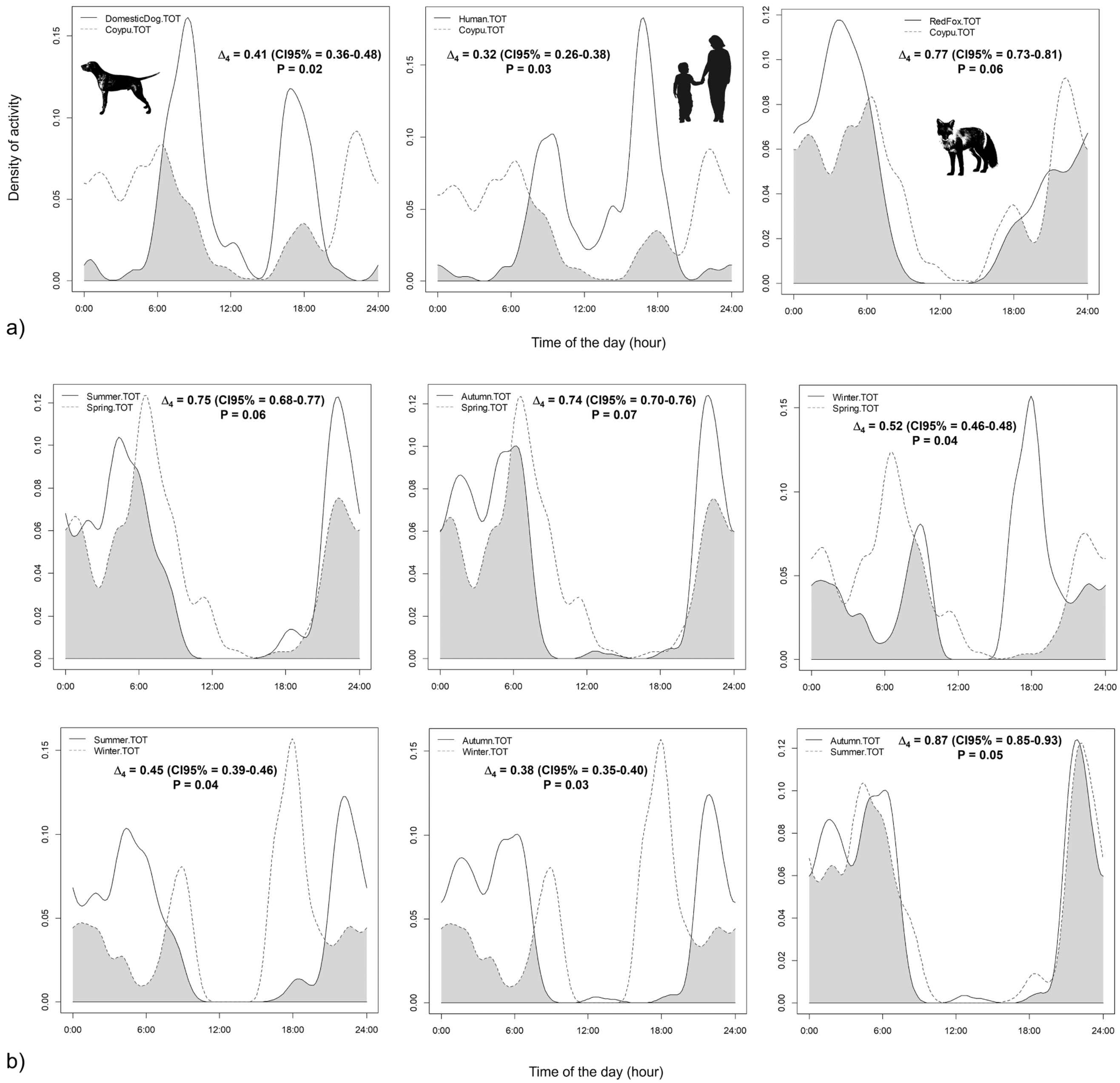


**Fig. 2.** a) Intraspecific seasonal overlap of coypu activity rhythms in Serravalle urban park; b) interspecific overlaps of activity rhythms between coypus and potential predators / competitors in Serravalle urban park (central Italy), assessed by camera trapping (N sites = 1) throughout 12 months.

7) Nose touching: winter (0.7 %) > spring (0.0 %) = summer (0.0 %) = autumn (0.0 %)
8) Parental cares: spring (0.8 %) > winter (0.6 %) > summer (0.0 %) = autumn (0.0 %)

### 3.2.3. *Activity budget per sex*

The comparative analysis of behaviour by sex (only adults and subadults) revealed distinct patterns. Females showed higher engagement in several activities compared to males. Specifically, females collected human-provided food more frequently than males (9.3 % *vs.* 4.3 %) and were also more active in eating in water (5.8 % *vs.* 3.9 %), foraging (12.4 % *vs.* 3 %), vigilance (2.5 % *vs.* 1.3 %) and exploring (12 % *vs.* 8.5 %). Additionally, females were the only sex to engage in nose touching, parental care and playing with kits. Females were also the only sex to exhibit aggressive behaviour and vocalisation.

In contrast, males were more involved in carrying objects (1.8 % *vs.* 0.7 %) and exhibited higher levels of self-grooming (30.6 % *vs.* 15.8 %) and scent-marking (5.6 % *vs.* 0.4 %: Fig. 4 and Table S2 in Supplementary Material 2).

### 3.2.4. *Activity budget per age class*

The analysis of behavioural patterns across different age classes revealed distinct trends (Fig. 4). Kits exhibited the highest levels of exploration and playing, significantly surpassing both subadults and adults. They also showed notable engagement in parental care. Additionally, kits showed higher frequencies of nose touching and vocalisation, all directed towards females (cfr. paragraph 3.2.3). Adults displayed more self-grooming compared to the other age classes. Behaviour such as aggressive behaviour, allogrooming, and scent marking were present primarily in adults and subadults, while being absent or minimal in kits (Fig. 4). These observations highlight the developmental differences in behaviour, with kits focusing on play

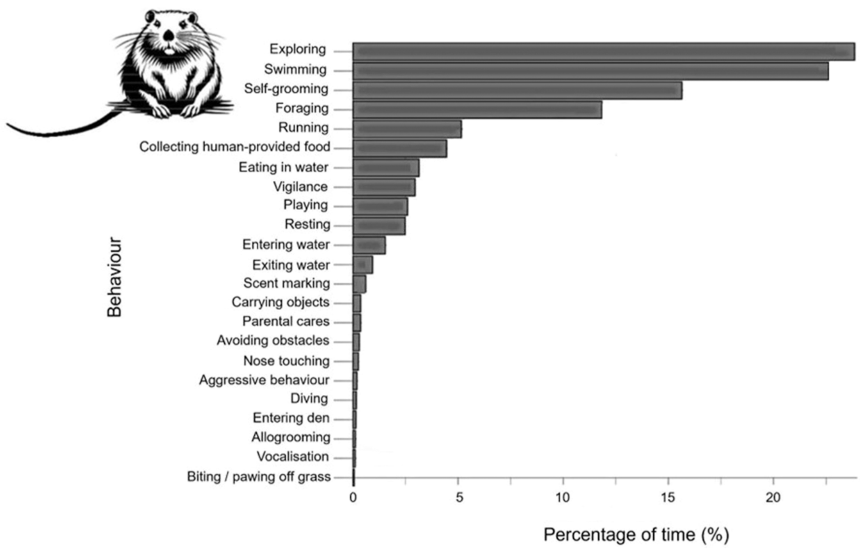


**Fig. 3.** Annual coypu activity budget in Serravalle Urban park (central Italy), quantified as percent time spent engaging in each classified behaviour, assessed by camera trapping (N sites = 1) throughout 12 months.

activities, subadults showing a balance of foraging and vigilance, and adults exhibiting more specialised behaviour related to self-maintenance and resource utilisation (Fig. 4 and Table S3 in Supplementary Material 2).

### 3.3. *Behavioural differences across age classes, sex, and seasons*

Estimated probabilities for sociable and distinctive behaviours across age classes, sex, and seasons were examined (Tables S4 and S5 in Supplementary Material 2).

#### 3.3.1. *Allo-grooming*

The GLM analysis did not show any significant effects of the age class, sex, or season variables. The observed allogrooming behaviour was very rare in most categories, with only minor distinctions found between the groups studied. Adults, females, and winter had a slightly higher probability, but differences were negligible (Tables S4 and S5 in Supplementary Material 2).

#### 3.3.2. *Self-grooming*

The GLM analysis revealed significant effects of age class and season on the probability of exhibiting self-grooming behaviour (Table S4 in Supplementary Material 2). In pairwise comparisons, the probability of self-grooming was significantly higher in adults compared to subadults, i.e., subadults engaged in self-grooming less frequently than adults. Adults exhibited a significantly higher probability of self-grooming also compared to kits. There was also a significant difference between subadults and kits, with kits showing a lower probability of self-grooming compared to subadults (Table S5 in Supplementary Material 2). Self-grooming behaviour was most common in adults, with both subadults and kits showing progressively lower probabilities, reflecting developmental changes in self-grooming behaviour across different age classes. In winter, the probability of self-grooming was significantly higher compared to all other seasons, and in spring it was significantly higher than in summer and autumn (Table S5 in Supplementary Material 2).

#### 3.3.3. *Nose touching*

GLM did not reveal any significant differences in nose touching behaviour across sex and season. The model considering age classes had an adjusted $R^2$ of 0.6 and showed significant differences among levels, with a greater probability that this behaviour will be adopted by kits rather than adults. (Tables S4 and S5 in Supplementary Material 2).

#### 3.3.4. *Parental cares*

The GLM analysis showed no significant effect of sex and season on parental care, while the age class showed a significant effect. Pairwise comparisons showed that kits were significantly more involved in this behaviour than adults ($\beta = 2.86$, $p = 0.0001$: Tables S4 and S5 in Supplementary Material 2).

#### 3.3.5. *Vigilance*

GLM analysis for sex and age class showed no significant effect on vigilance (Table S4 in Supplementary Material 2), while the season had a significant effect. Pairwise comparisons revealed that the probability of this behaviour occurring is significantly lower in winter compared to all other seasons, and in autumn compared to summer (Table S5 in Supplementary Material 2).

#### 3.3.6. *Scent marking*

GLM results showed a significant effect of sex, with males being more likely to exhibit this behaviour compared to females. Conversely, neither the age class nor the season influenced the probability of this behaviour (Table S4 in Supplementary Materials 2).

#### 3.3.7. *Playing*

The GLM analysis indicated that sex does not significantly impact playing behaviour (Table S4 in Supplementary Material 2). Regarding the age class and season, GLM revealed a significant effect on playing behaviour. The pairwise comparisons showed that subadults are more likely to exhibit this behaviour compared to adults, and kits are more likely to do so compared to both adults and subadults. Finally, the probability of observing play behaviour was significantly lower in winter compared to all other seasons (Table S5 in Supplementary Material 2).

## 4. Discussion

This research investigates the behaviour of coypu, an invasive alien mammal, in an urban environment of central Italy (Viviano et al., 2024). We provided support to the prediction that coypus are well adapted to human presence and urban ecosystems, exhibiting high levels of nocturnal activity, peaking at dawn and dusk (prediction *i*). This suggests a reduced perceived predation risk compared to natural ecosystems, and a significant temporal segregation from diurnal anthropic activities for reducing the risk to encounters with humans and unleashed

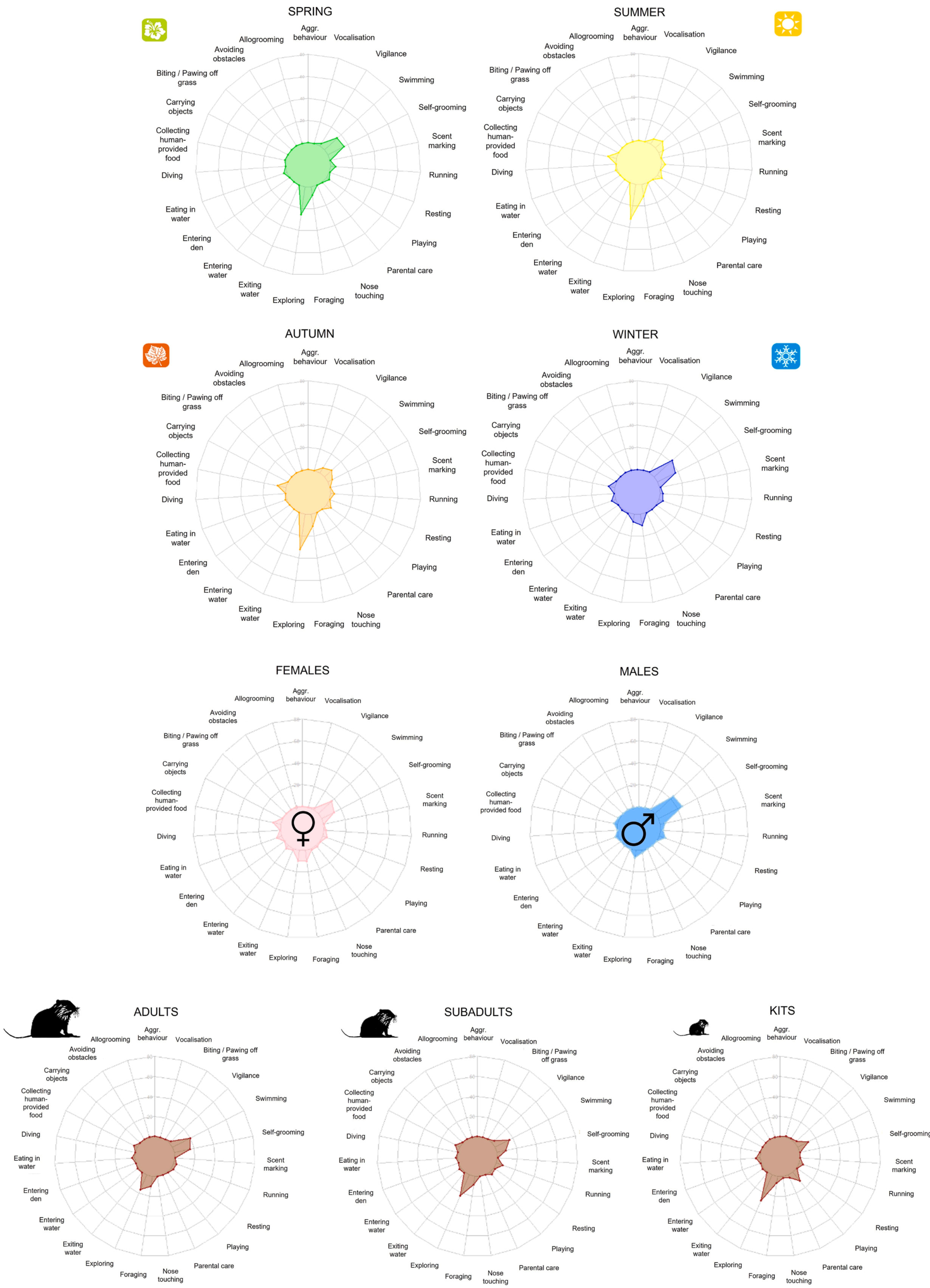


**Fig. 4.** Radar chart plots of coypu behaviour patterns across the four seasons (spring, summer, autumn, and winter), sexes (males and females), and age classes (adults, subadults, and kits) in Serravalle Urban Park (central Italy), as assessed by camera trapping (N sites = 1) throughout 12 months. Peaks show differences across seasons, sexes and age classes, as reported in the main text.

dogs (Mori et al., 2020b; Salas et al., 2022). Conversely, in a comparable urban area of central Europe, coypus were mostly active in daylight hours, when humans used to feed them (Meyer et al., 2005). Coypus are fed by humans in Serravalle urban park too, but this behaviour mostly occurred at dawn and dusk, and we never observed it during the central part of the day, a factor possibly preventing a more diurnal behaviour of coypus in our study area. Activity patterns showed moderate to high seasonal overlap, except for winter, with activity concentrated in early morning and late afternoon, in line with previous works on the species (Meyer et al., 2005; Mori et al., 2020a, b; Poláčková et al., 2022; Salas et al., 2022). A reduction in nocturnal behaviour was recorded in winter, when nights are the coldest, potentially representing a compensation mechanism towards more suitable environmental temperatures (Chabrek, 1962, Gosling et al., 1980). Throughout the year, nocturnal activity was lowest during bright moonlight nights, suggesting potential lunar phobia as an anti-predatory strategy (Michalski and Norris, 2011; Mori et al., 2020a). Coypu activity overlapped most with red foxes (Koynova et al., 2023), a potential predator, and least with humans with unleashed dogs, which likely represent a considerable threat to coypus (cfr. Meyer et al., 2005; Sogliani et al., 2023). This may be explained by either a low perceived risk of predation from the red fox by the local population of coypus (which is actually known to be occasional), or because resident foxes may exploit other - easier - food resources such as garbage and food waste by park visitors, thus reducing the attractiveness of wild prey such as coypus (as seen by Panek and Budny, 2017).

Our second hypothesis (prediction *ii*) was likewise supported: coypus inhabiting urban areas exhibited a significantly broader behavioural repertoire compared to those in captivity and in rural areas (Gosling, 1979; Poláčková et al., 2022; Salas et al., 2022). This result may be likely due to the small area occupied by coypus in our study, leading to high detectability of their entire behavioural repertoire. Alternatively, genuinely higher numbers of behaviours may also be due to the favourable conditions of urban parks, that provide plenty of opportunities for food and lower predation pressure in comparison to natural areas (Eötvös et al., 2018), both factors potentially fostering e.g., higher social activities in coypus.

Our study is based on a single sampled site, whose small size allowed us to adopt a single-station sampling strategy. We are aware of the potential limitations deriving from such a limited effort, and call for caution in over-generalising our results. Nonetheless, by covering the entire area of interest and conducting a year-round, 24/7 sampling, we are confident that our results genuinely represent the local population's behaviour, and may serve as a model for other studies and contexts. As such, our findings corroborate the efficacy of camera traps in elucidating the behaviour of a highly camera-trappable species in urban areas (prediction *iii*). Exploring, swimming, self-grooming (mostly by adults and subadults in winter and spring), and foraging were the most frequently observed behavioural patterns. Parental cares were mostly female prerogatives towards dependent young, peaking in summer, when kits are present, as typical of most polygynous gregarious mammals, and significantly declining in winter (Zeveloff and Boyce, 1980; Guichón et al., 2003b; Schubert et al., 2009). Accordingly, vigilance by both adult males and females significantly increased in summer, when kits are present, and predation risk is higher, due to lower water levels. Scent marking, which occurred both in water upon surfacing rocks and branches and on land, was strictly an adult male behaviour, as only male coypus are territorial (Gosling and Wright, 1994). Aggressive behaviour was rarely observed and it was only exerted by adult females against other coypus, geese and red foxes, peaking in summer, when coypus start to defend kits and dens. Accordingly, all individuals exhibiting injuries (partial tail amputations, or scars) were identified as females, suggesting a defensive role of female coypu in protecting their offspring and dens against potential predators and competitors. This hypothesis is also confirmed by the higher level of vigilance shown by females in comparison to males.

Coypu social groups exhibit high social cohesion and fidelity and have been described in the literature as engaging in positive interindividual interactions, particularly between females and juveniles. In the native range (South America), cooperative behaviours within the group have been recorded (Guichón et al., 2003b). Despite this gregarious behaviour, in our study site, vocalisations were only rarely recorded, and always produced by females and kits, possibly as part of parental care or for maintaining contact from a distance. Play primarily occurred among kits (or between kits and adult females) and was predominantly locomotor, consisting of ambushes, driving-drills and chases. Play which mimics adult aggression (named "playing wrestling" for beaver kits: Bau, 2001) has only been recorded on two occasions in our study (Herrera et al., 2021).

This study provides valuable insights into coypu behaviour in an urban environment. Although we acknowledge the limitations of our methods, increasing the number of camera stations would have been challenging due to a lack of suitable sites and legal privacy constraints in urban areas (Herrera et al., 2021; Italian Legal Decree 196, 30/06/2003). Moreover, in our study area, additional stations were unnecessary as all dens used were already within our camera trap detection range.

The individuals observed likely belonged to the same family group, facilitating the identification of different animals. To confirm our findings on a larger scale, more intensive studies should be conducted on larger populations. Understanding these behavioural patterns enables wildlife managers to develop more effective and sustainable strategies for managing invasive species in urban areas, raising public awareness, and promoting responsible human-wildlife coexistence (Evans, 1970). For example, our findings indicate that the predominantly nocturnal activity of coypu may warrant night-time interventions to minimise conflicts with people.

Apart from small, isolated populations, the eradication of coypu at large scale is considered as no longer technically feasible in peninsular Italy (see Bertolino et al., 2005; Panzacchi et al., 2007; Bertolino and Cocchi, 2018). Therefore, control programs are underway in northern and central regions to mitigate impacts on native biodiversity and human activities/infrastructures (Bertolino and Cocchi, 2018). The species' high ecological plasticity is likely key to its success as a biological invader, allowing it to colonise a wide range of environments, from natural ponds to wetlands and urban areas. The success control campaigns of coypu are highly dependent upon local population density, as well as social behaviour and spatiotemporal ecology, which should be assessed prior to intervention. Within the Serravalle urban park, the high population density has led to extensive burrowing, potentially compromising the stability of the pond banks over time (Dondina et al., 2024). Given the coypu nocturnal behaviour and high sociability, trapping efforts are recommended to be concentrated after dusk, near the water edge, and preferably during the warmer months (July to October) when water levels are the lowest.

## Funding

LA, OD and EM was funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4- Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – Next Generation EU; Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B83C22002930006, Project title "National Biodiversity Future Center—NBFC".

## CRediT authorship contribution statement

**Dondina Olivia:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Burchielli Alice:** Investigation, Formal analysis, Data curation. **Viviano Andrea:** Writing – review & editing, Writing –

original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Ancillotto Leonardo:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation, Conceptualization. **Miccolis Daniela:** Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Mori Emiliano:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## 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.

## Acknowledgements

Authors would like to thank the Empoli Municipality Council (in particular, Fabio Barsottini), who allowed us to conduct this research study in the Serravalle urban park. Chiara Giubbani and Valerio Giorgio Muzzini kindly helped us with Italian ethics and privacy laws. Professor Filippo Barbanera (University of Pisa) provided us with useful comments and helped in data analysis.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2025.106534.

## Data availability

Data used in this study are available in the Supplementary Materials.

## References

Amori, G., Contoli, L., Nappi, A., 2008. Mammalia II: Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. Il Sole 24 Ore. Edagricole, Calderini, Bologna, Italy.

Ancillotto, L., Amori, G., Capizzi, D., Cignini, B., Zapparoli, M., Mori, E., 2024. No city for wetland species: habitat associations affect mammal persistence in urban areas. Proc. R. Soc. B 291, 20240079.

Baker, S., 2006. The eradication of coypus (*Myocastor coypus*) from Britain: the elements required for a successful campaign. In: Koike, F., Clout, M.N., Kawamichi, M., De Poorter, M., Iwatsuki, K. (Eds.), Assessment and Control of Biological Invasion Risks. Shoukadoh Book Sellers. Japan and IUCN, Gland, Switzerland, Kyoto, pp. 142–147.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bau, L.M., 2001. Behavioural ecology of reintroduced beavers (*Castor fiber*) in Klosterheden State Forest, Denmark. Master Thesis, Department of Animal Behaviour, University of Copenhagen, Copenhagen, Denmark.

Bertolino, S., Angelici, C., Monaco, E., Monaco, A., Capizzi, D., 2011. Interactions between coypu (*Myocastor coypus*) and bird nests in three Mediterranean wetlands of central Italy. Hystrix 22, 333–339.

Bertolino, S., Cocchi, R., 2018. Piano di gestione nazionale della Nutria *Myocastor coypus*. Ministero dell'Ambiente e della Tutela del Territorio e del Mare, ISPRA. Technical Report, Roma and Ozzano nell'Emilia (Bologna), Italy.

Bertolino, S., Genovesi, P., 2007. Semiaquatic mammals introduced into Italy: case studies in biological invasion. In: Gherardi, F. (Ed.), Biological invaders in inland waters: Profiles, distribution, and threats. Springer Editions, Dordrecht, Netherlands, pp. 175–191.

Bertolino, S., Perrone, A., Gola, L., 2005. Effectiveness of coypu control in small Italian wetland areas. Wildl. Soc. Bull. 33, 714–720.

Carboneras, C., Genovesi, P., Vila, M., Blackburn, T.M., Carrete, M., Clavero, M., D'hondt, B., Orueta, J.F., Gallardo, B., Geraldes, P., Gonzalez-Moreno, P., Gregory, R.D., Nentwig, W., Paquet, J.Y., Pysek, P., Rabistsch, W., Ramirez, I., Scalera, R., Tella, J.L., Walton, P., Wynde, R., 2018. A prioritised list of invasive alien species to assist the effective implementation of EU legislation. J. Appl. Ecol. 55, 539–547.

Carter, J., Leonard, B.P., 2002. A review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor coypus*). Wildl. Soc. Bull. 30, 162–175.

Chabrek, R.H., 1962. Daily activity of nutria in coastal Louisiana. J. Mammal. 43, 337–344.

Cocchi, R., Riga, F., 2001. Guidelines for the control of coypu (*Myocastor coypus*). Quaderni di Conservazione della Natura. Ministero Ambiente e Istituto Nazionale per la Fauna Selvatica, Italy, p. 189. Vol. 5.

Corriale, M.J., Arias, S.M., Bó, R.F., Porini, G., 2006. Habitat-use patterns of the coypu *Myocastor coypus* in an urban wetland of its original distribution. Acta Theriol. 51, 295–302.

Cosma, R., 2001. Biometrics and age assessment in the crested porcupine *Hystrix cristata* L., 1758. Tesi di Laurea, Università degli Studi di Siena, Siena, Italy [in Italian].

D'Adamo, P., Guichon, M.L., Bó, R.F., Cassini, M.H., 2000. Habitat use of coypus (*Myocastor coypus*) in agro-systems of the Argentinean Pampas. Acta Theriol. 45, 25–33.

Dell'Agnello, F., Martini, M., Mori, E., Mazza, G., Mazza, V., Zaccaroni, M., 2020. Winter activity rhythms of a rodent pest species in agricultural habitats. Mammal. Res 65, 69–74.

Dias, D.M., Massara, R.L., de Campos, C.B., Rodrigues, F.H.G., 2019. Feline predator-prey relationships in a semiarid biome in Brazil. J. Zool. 307, 282–291.

Doncaster, C.P., Micol, T., 1989. Annual cycle of a coypu (*Myocastor coypus*) population: male and female strategies. J. Zool. 217, 227–240.

Dondina, O., Orioli, V., Tirozzi, P., Bani, L., 2024. Estimating risk to prevent damage: predicting and preventing coypu (*Myocastor coypus*) damage to transport infrastructure. Pest Manag. Sci. 80, 5564–5573.

Eötvös, C.B., Magura, T., Lövei, G.L., 2018. A meta-analysis indicates reduced predation pressure with increasing urbanization. Landsc Urb. Plan. 180, 54–59.

Evans, J., 1970. About nutria and their control. US Fish. Wildl. Serv. Res. Publ. 86, 1–65.

Fitak, R., Johnsen, S., 2020. Package 'CircMLE'. Maximum Likelihood Analysis of Circular Data. Available at: https://CRAN.R-project.org/package=CircMLE. Accessed on 04.08.2024.

Gosling, L.M., 1979. The twenty-four hour activity cycle of captive coypus (*Myocastor coypus*). J. Zool. 187, 341–367.

Gosling, L.M., Guyon, G.E., Wright, K.M., 1980. Diurnal activity of feral coypus (*Myocastor coypus*) during the cold winter of 1978-9. J. Zool. Lond. 192, 143–146.

Gosling, L.M., Wright, K.H.M., 1994. Scent marking and resource defence by male coypus. J. Zool. Lond. 234, 423–436.

Guichón, M.L., Benitez, V.B., Abba, A., Borgnia, M., Cassini, M.H., 2003a. Foraging behaviour of coypus *Myocastor coypus*: why do coypus consume aquatic plants? Acta Oecol 24, 241–246.

Guichón, M.L., Borgnia, M., Righi, C.F., Cassini, G.H., Cassini, M.H., 2003b. Social behavior and group formation in the coypu (*Myocastor coypus*) in the Argentinean Pampas. J. Mammal. 84, 254–262.

Herrera, D.J., Moore, S.M., Flockhart, D.T.T., McShea, W.J., Cove, M.V., 2021. Thinking outside the park: recommendations for camera-trapping mammal communities in the urban matrix. J. Urb. Ecol. 6, 1–13.

Hosey, G.R., 2005. How does the zoo environment affect the behaviour of captive primates? Appl. Anim. Behav. Sci. 90, 107–129.

James, G., Witten, D., Hastie, T., Tibshirani, R., 2021. Moving beyond linearity, in an introduction to statistical learning: with applications. In: In: James, R., Witten, G., Hastie, D., Tibshirani, R., T. (Eds.), Springer Texts in Statistics. Springer US, New York, NY, pp. 289–326.

Kil, J., Lee, D.H., Kim, Y.C., 2015. Effective management of invasive nutria (*Myocastor coypus*) in the UK and the USA. Ecol. Resil. Infrastr. 2, 265–273.

Koynova, T., Tsvetkov, R., Natchev, N., 2023. A fox on the hunt: red fox (*Vulpes vulpes*) was able to subdue and kill an adult coypu (*Myocastor coypus*) in a protected site in south-eastern Bulgaria. Nat. Croat. 32, 549–554.

Ladent, E., Leriche, A., Thomas, B., Millon, A., 2022. Weak evidence of spatial segregation between the vulnerable southern water vole (*Arvicola sapidus*) and the two main invasive mammals of European freshwater ecosystems. Ecosci 29 (2), 147–158.

Landler, L., Ruxton, G.D., Malkemper, E.P., 2019. The Hermans–Rasson test as a powerful alternative to the Rayleigh test for circular statistics in biology. BMC Ecol. 19, 1–8.

Lenth, R.V., 2024. emmeans: Estimated Marginal Means, aka Least–Squares Means. Available at: https:// CRAN.R–project.org/package=emmeans. Accessed on 27.08.2024.

Linkie, M., Ridout, M.S., 2011. Assessing tiger–prey interactions in Sumatran rainforests. J. Zool. 284, 224–229.

Lovari, S., Mori, E., Procaccio, E.L., 2020. On the behavioural biology of the mainland serow: a comparative study. Animals 10, 1669.

Lund, U., Agostinelli, C., Arai, H., Gagliardi, A., Portugues, E.G., Giunchi, D., Irisson, J. O., Pocernich, M., Rotolo, F., 2017. Package circular. Available at: https://mirro rs.ucr.ac.cr/CRAN. Accessed on 04.08.2024.

Mason, G., Burn, C.C., Dallaire, J.A., Kroshko, J., Kinkaid, H.M., Jeschke, J.M., 2013. Plastic animals in cages: behavioural flexibility and responses to captivity. Anim. Behav. 85, 1113–1126.

Massara, R.L., Paschoal, A.M.O., Bailey, L.L., Doherty, P.F., Barreto, M.F., Chiarello, A.G., 2018. Effect of humans and pumas on the temporal activity of ocelots in protected areas of Atlantic Forest. Mammal. Biol. 92, 86–93.

McLeod, L.J., Hine, D.W., Please, P.M., Driver, A.B., 2015. Applying behavioral theories to invasive animal management: towards an integrated framework. J. Env. Manag. 161, 63–71.

Meredith, M., Ridout, M., 2021. Overview of the overlap package. R. Proj. 2014, 1–9.

Meyer, J., Klemann, N., Halle, S., 2005. Diurnal activity patterns of coypu in an urban habitat. Acta Theriol. 50, 207–211.

Michalski, F., Norris, D., 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. Zool. (Curitiba) 28, 701–708.

Monterroso, P., Alves, P.C., Ferreras, P., 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav. Ecol. Sociobiol. 68, 1403–1417.
Mori, E., Andreoni, A., Cecere, F., Magi, M., Lazzeri, L., 2020a. Patterns of activity rhythms of invasive coypus *Myocastor coypus* inferred through camera-trapping. Mammal. Biol. 100, 591–599.
Mori, E., Sangiovanni, G., Corlatti, L., 2020b. Gimme shelter: the effect of rocks and moonlight on occupancy and activity pattern of an endangered rodent, the garden dormouse *Eliomys quercinus*. Behav. Process. 170, 103999.
O'Connell, A.F., Nichols, J.D., Karanth, K.U., 2011. Camera traps in animal ecology. Methods and analyses. Springer, New York, USA.
Panek, M., Budny, M., 2017. Variation in the feeding pattern of red foxes in relation to changes in anthropogenic resource availability in a rural habitat of western Poland. Mammal. Biol. 82, 1–7.
Panzacchi, M., Cocchi, R., Genovesi, P., Bertolino, S., 2007. Population control of coypu *Myocastor coypus* in Italy compared to eradication in UK: a cost-benefit analysis. Wildl. Biol. 13, 159–171.
Poláčková, I., Šerá, B., Jureček, R., Pavličková, K., 2022. The daily and seasonal behaviour of the American mink and the coypu, two invasive species from the Záhorie PLA (Slovakia). Acta Ethol. 25, 115–123.
Pyšek, P., Richardson, D.M., 2010. Invasive species, environmental change and management, and health. Annu. Rev. Environ. Res. 35, 25–55.
R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/ Accessed on 04.08.2024.
Reggiani, G., Boitani, L., De Stefano, R., 1995. Population dynamics and regulation in the coypu *Myocastor coypus* in central Italy. Ecogr 18, 138–146.
Reynolds, P., 1979. Preliminary observations on the food of the fox (*Vulpes vulpes* L.) in the Camargue, with special reference to rabbit (*Oryctolagus cuniculus* L.) predation. M. ammalia 43, 295–307.
Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agr. Biol. Environm. Stat. 14, 322–337.
Ruys, T., Lorvelec, O., Marre, A., Bernez, I., 2011. River management and habitat characteristics of three sympatric aquatic rodents: common muskrat, coypu and European beaver. Eur. J. Wildl. Res. 57, 851–864.
Salas, M., Hernandez-Hernandez, J.C., Iglesias, M., Corriale, M.J., 2022. Activity patterns and behavior of *Myocastor coypus* in a gated community in the metropolitan area of Buenos Aires (Argentina). J. Urb. Ecol. 8, juab037.
Schertler, A., Rabitsch, W., Moser, D., Wessely, J., Essl, F., 2020. The potential current distribution of the coypu (*Myocastor coypus*) in Europe and climate change induced shifts in the near future. NeoBiota 58, 129–160.
Schubert, M., Pillay, N., Schradin, C., 2009. Parental and alloparental care in a polygynous mammal. J. Mammal. 90, 724–731.
Sogliani, D., Mori, E., Lovari, S., Lazzeri, L., Longoni, A., Tabarelli De Fatis, K., Sabatini, P., Di Nicola, M.R., Russo, D., 2023. Citizen science and diet analysis shed light on dog-wildlife interaction in Italy. Biodivers. Conserv. 32, 4461–4479.
Viviano, A., De Meo, I., Mori, E., Sergiacomi, C., Paletto, A., 2024. Public perception and acceptance of coypu *Myocastor coypus* removal in urban areas: influences of age and education. Sci. Nat. 111, 42.
Wand, M.P., Jones, M.C., 1994. Kernel Smoothing. CRC press. Chapman & Hall Editions, London, UK.
Wickham, H., Francois, R., Henry, L., Müller, K., 2014. dplyr. A Grammar of Data Manipulation 2020. Available at: https://cran.r-project.org/web/packages/dplyr/dplyr.pdf. Accessed on 04.08.2024.
Zeveloff, S.I., Boyce, M.S., 1980. Parental investment and mating systems in mammals. Evol 34, 973–982.
Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing ecological data (Vol. 680). Springer Editions, New York, USA.