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Back to the river: Behavioural patterns of Eurasian beavers recolonising central Italy

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ABSTRACT

Newly introduced species may alter the structure and functioning of colonised ecosystems, particularly when they act as ecosystem engineers. The Eurasian beaver *Castor fiber*, historically present in central Italy until the Middle Ages, has recently reappeared in the region. Despite growing evidence of its ecological impacts, detailed information on its behavioural repertoire in Mediterranean environments is lacking. Here, the first comprehensive behavioural assessment of Eurasian beavers recolonising central Italy using intensive camera trapping across three river systems is provided. From March 2023 to May 2024, 24 distinct behavioural patterns were recorded and their occurrence and duration were quantified across age classes, sex, and seasons. Behavioural expression was strongly age-dependent: juveniles showed significantly higher levels of play, allogrooming, nose-touching, and exploratory behaviour, while subadults exhibited increased diving and exploration, indicating a transition towards independence. Adults displayed a broader and more functional repertoire, with higher frequencies of swimming, vigilance, scent marking, and material transport on land, reflecting their role in territory maintenance and construction activities. Seasonality also shaped behaviour markedly. Dam-building and digging activities and swimming were significantly more frequent during the cold period, whereas self-grooming sharply increased during warm period, suggesting thermally-driven behavioural plasticity. Model comparisons revealed that social and developmental behaviours were best explained by age, whereas construction and maintenance behaviours were primarily driven by seasonal conditions. Compared with northern European populations, Italian beavers showed lower building frequencies but increased terrestrial and swimming activities, suggesting context-dependent behavioural adjustments shaped by local ecological conditions.

1. Introduction

The assessment of animal behaviour is essential for effective species management and conservation, as behavioural studies help clarify ecological roles and social structures which can directly have an influence on population dynamics (Stanton et al., 2015; Viviano et al., 2025). A lack of behavioural knowledge may result in poorly designed conservation actions (including protection and management), which fail to account for species-specific requirements, potentially leading to ineffective or even harmful interventions (Singh and Kaumanns, 2005). Understanding time budgets and activity patterns can contribute to the development of effective management strategies based on animal ecology, to reduce human–wildlife conflicts and enhance the persistence of species of conservation concern (Blackwell et al., 2016; Greggor et al., 2019; Dell'Agnello et al., 2020; Viviano et al., 2025). For instance, the most efficient trapping programmes for the Savi's pine vole *Microtus savii* should take place in daylight hours to reduce stress levels of captured animals (Dell'Agnello et al., 2020). Ethological research also informs habitat protection and restoration by identifying behavioural patterns linked to specific environmental conditions, e.g., breeding triggers and foraging strategies (LaPoint et al., 2013; Stanton et al., 2015; Viviano et al., 2025).

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Amongst species needing both conservation measures and mediation strategies of human-wildlife conflict, the Eurasian beaver *Castor fiber* is currently re-expanding throughout Europe following legal protection and reintroduction efforts (Halley et al., 2021). In the last 30 years, the species has recolonised areas where it went historically absent, and has increased its local population density where it has always been present (Halley et al., 2021). This has led to conflicts with human activities, highlighting the need for management actions designed to mitigate impacts and support coexistence between humans and wildlife (Swinnen et al., 2017).

Conflicts with beavers arise primarily due to their dam-building behaviour, which can lead to flooding of roads, agricultural fields, and residential areas (Mikulka et al., 2020; Nica et al., 2022). Beavers are also known as tree-cutters, which can result in damage to valuable timber and landscaping (Swinnen et al., 2017; Pașca et al., 2022). The most common approaches for coexistence include installing flow devices to regulate water levels without removing beaver dams, using tree protection measures like wire mesh, and, in some cases, relocation or population control (Nolet and Rosell, 1998; Wróbel and Krysztofiak-Kaniewska, 2020). Non-lethal approaches which focus on modifying beaver behaviour and site use seems to be more effective than controlling population size (Rosell and Campbell-Palmer, 2022). Such behaviour-based measures allow conflicts to be reduced while maintaining the ecological benefits provided by beavers, including increased biodiversity, forest regeneration, and water regulation (Rosell et al., 2005).

Empirical data on beaver ethology are extremely limited and lack recent updates (e.g., Tevis, 1950; Schramm, 1968; Hodgdon and Larson, 1973; Patenaude and Bovet, 1984). Despite an exhaustive review of the literature, no recent or comprehensive investigations addressing this aspect was found. Accordingly, the behavioural repertoire of the Eurasian beaver has been only partially described by Bau (2001) in a reintroduced population in central Denmark, through direct observations. These data were then further integrated with other observations conducted in naturally recolonising beaver populations (e.g., Sharpe and Rosell, 2003; Rosell and Campbell-Palmer, 2022), as well as with published literature on North American beaver (Tevis, 1950; Schramm, 1968; Hodgdon and Larson, 1973; Patenaude and Bovet, 1984; Gallant et al., 2016), to describe a compilation of seventeen behavioural patterns for both species. Both beaver species are behaviourally very similar, but some differences may occur: North American beavers often show a higher propensity to build dams and slightly different habitat-use and scent-marking/territorial patterns where the two species interact (Danilov and Kanshiev, 1983; Rosell and Campbell-Palmer, 2022).

Beavers are mostly nocturnal monogamous species, with secretive, semifossorial and semiaquatic habits (Bartra Cabre et al., 2020; Mortensen et al., 2021; Mori et al., 2022a), thus limiting the potential to exhaustively describe their behavioural repertoire through direct observations from vantage points. Assessing beaver behaviour is especially important in regions with frequent interactions with human activities and in areas where Eurasian beavers represent a recent arrival. A recent work on coypus *Myocastor coypus* (Viviano et al., 2025) suggested that camera traps may provide a more comprehensive assessment of behavioural patterns of nocturnal rodents compared to direct observations, e.g., detecting (mostly nocturnal) behaviours not previously recorded by direct observation studies.

The recent reappearance of beavers in this central Italy after centuries of absence (in 2020: Mori et al., 2024) provides a unique, unplanned "natural experiment" to examine how a powerful ecosystem engineer adapts its behaviour under environmental conditions which differ markedly from those of its core European range. Behavioural plasticity is a key mechanism underlying successful establishment and spread, yet no study has previously quantified the full behavioural repertoire, activity budgets, or behavioural drivers of Eurasian beavers in a Mediterranean environment. Furthermore, effective management of human–beaver conflicts and prediction of ecological impacts require an understanding of when, how, and by which age classes behaviours such as construction, exploration, and social interactions are performed (Falaschi et al., 2024). Without a comprehensive assessment of quantitative behavioural data, management actions could be poorly timed or misdirected.

By combining intensive camera trapping with a structured ethogram and statistical modelling, this study provided the first comprehensive, year-round, and age-structured behavioural assessment of Eurasian beavers in central Italy. In doing so, it establishes a necessary baseline for both comparative ethology and evidence-based management of a rapidly expanding ecosystem engineer in southern Europe. It was predicted that (i) camera trap data will show higher activity levels during nighttime compared to daytime (in line with Mori et al., 2022a) and that (ii) beavers will exhibit seasonal variations in activity, with increased foraging in autumn and winter due to food storage needs. Recently recolonising populations of *Castor fiber* in Central Italy may exhibit some differences in behavioural patterns compared to northern European populations (Bau, 2001), driven by differences in predation pressure, river characteristics, and interspecific competition (Mori et al., 2022a,b; Falaschi et al., 2024).

2. Materials and methods

2.1. Study area

This study was conducted in two river basins in the Tuscany region of central Italy: the Ombrone-Merse basin, encompassing the provinces of Siena and Grosseto (for about 130 km of rivers), and the Tevere basin, covering Anghiari and Sansepolcro municipalities in the province of Arezzo (for about 20 km of rivers: Fig. 1). Since 2019–2020, at least 30–50 individual Eurasian beavers have been detected in these areas (Mori et al., 2024). The primary habitat consists of deciduous riparian woodlands (87 %), dominated by *Salix eleagnos* Scop., *Populus nigra* L., *Populus alba* L., *Alnus glutinosa* L. (Gaertn.), *Fraxinus ornus* L., and *Cornus mas* L. Additionally, non-native species such as *Robinia pseudoacacia* L. and *Acer negundo* L. are present and expanding (Mori et al., 2022a). In the Ombrone-Merse basin, all beaver records occurred in the main rivers, despite the occurrence of few natural ponds. In the Tevere river basin, over 90 % records occurred in the main river, two in a small stream (Cerfone) and three in small ponds near Sansepolcro (Golena del Tevere Natural Park). The local climate is predominantly humid, with warm summer months (26.9 ± 3.4 °C) and relatively mild winter months (8.4 ± 3.1 °C). Most precipitation occurring in autumn and winter, averaging 1123 ± 220 mm in 2023–2024 (see Sensi et al., 2020; Di Lorenzo et al., 2024). In central Italian rivers, summer low-flow conditions lead to reduced discharge, water level, and flow velocity, with stronger effects in Ombrone/Merse than in Tevere, whose regime is partially regulated by the Montedoglio dam upstream (Preti et al., 2025). Study rivers drain structurally complex Apennine landscapes, flowing from hilly areas dominated by metamorphic and sedimentary bedrock into wider alluvial valleys shaped by Quaternary fluvial deposits, with the Ombrone developing an extensive lowland floodplain in its lower course (Sensi et al., 2020; Mori et al., 2022a).

The grey wolf *Canis lupus* is the only large predator in the study area, with at least one pack of 4–6 individuals in both the Ombrone-Merse and Tevere river basins (Mori et al., 2022b). The mesocarnivore community includes the red fox *Vulpes vulpes*, the most abundant carnivore, the wildcat *Felis silvestris*, the European badger *Meles meles*, the stone marten *Martes foina*, the pine marten *Martes martes* and the least weasel *Mustela nivalis* (Viviano et al., 2022).

2.2. Camera trapping

Data were collected between March 2023 and May 2024 using camera traps (Browning SpecOps©, $n = 10$) deployed at 14 fixed, georeferenced stations (Fig. 1; Mori et al., 2024), 13 located along the

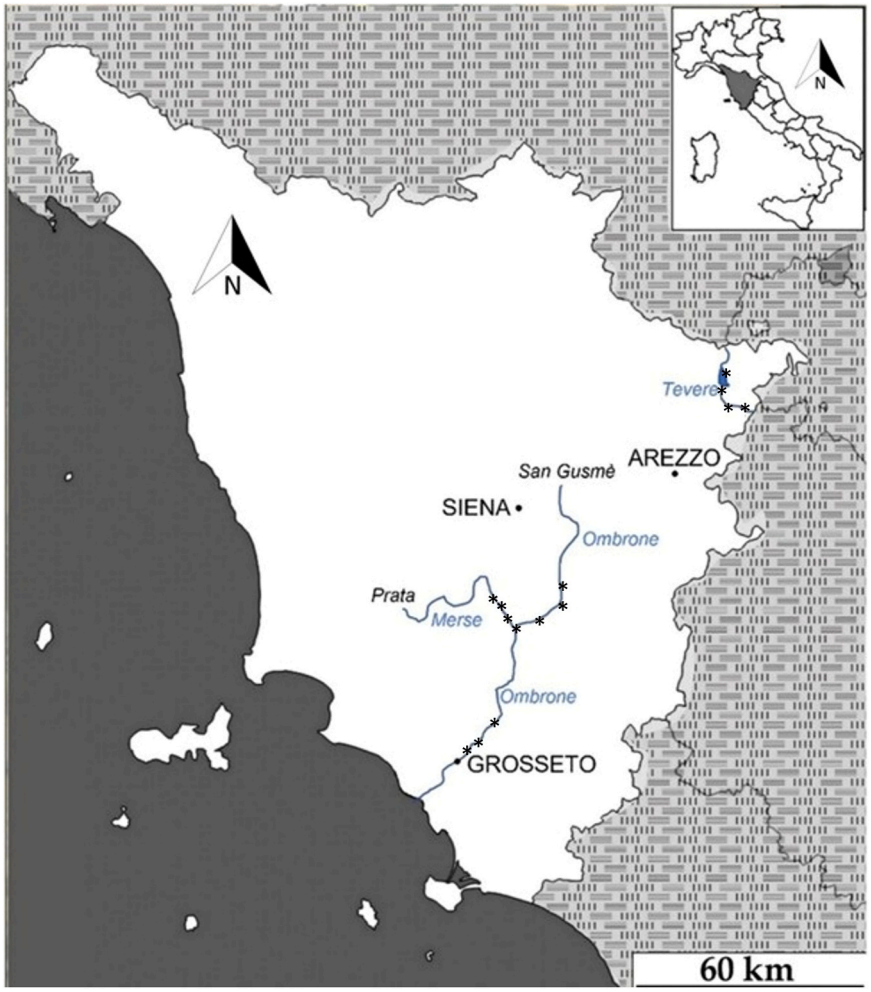

Fig. 1. Location of the study area (central Italy). Asterisks refer to camera-trap stations.

main rivers, and one placed on the shore of a pond near the Tiber River. This camera trap brand includes a high trigger speed (< 1 sec), which is pivotal to minimise the risk of missing parts of the behavioural sequences captured on camera traps (Viviano et al., 2025).

Stations were opportunistically selected based on recent beaver activity, such as dams and lodges, all situated outside protected areas. Except for two cameras placed near a dam, the rest were positioned directly in front of known burrows or lodges to record the first emergence of individuals. To ensure spatial independence of records, stations were spaced at least 800–1000 m from one another, given that, besides dispersing subadults, adult beavers daily ranges for about 200–1000 m (Herr and Rosell, 2004; Bartra Cabre et al., 2020). Cameras, mounted 50–80 cm above ground level, operated continuously (24 h/day, 7 days a week), recording 60-second videos per activation. All cameras were checked every 30 days for data retrieval and battery replacement, and rotated between stations once every 100 nights. Each station was monitored for 45–50 nights per season, with the shortest duration occurring when a beaver felled the tree where a camera was mounted (i.e., 27 nights, for the last sampling season). No significant temporal bias was detected in seasonal station sampling (Rayleigh test: $Z = 12.50$, $p = 0.08$). All recorded data were compiled into a dataset including variables such as "number of individuals," "date," "time," "station," and "season" (spring, summer, winter and autumn). Beavers were categorised into age classes based on body size, distinguishing between adults, subadults, and juveniles (see Mori et al., 2022a; Hinds et al., 2023). Juvenile beavers are usually defined as “kits”. If an individual age class could not be determined, it was labeled as ND ("not determined"). Determining an age class from camera trap footage can be challenging. However, since fixed camera stations were used and both adults and kits were detected at each station, subadults were arbitrarily defined as animals displaying an intermediate size between adults and kits (Cosma, 2001; Mori et al., 2025; Viviano et al., 2025). In cases where only a single animal appeared in a video, frames were compared by overlaying them with frames from other videos from the same camera trap, always using beavers for reference (Cosma, 2001).

Sex determination was conducted only for sexually mature individuals, through the observation of primary sexual characteristics (penis, testes) or prominent nipples during lactation. No distinguishing traits (e.g., truncated tails or visible scars: Dytkowicz et al., 2023; Viviano et al., 2025) were present in camera-trapped beavers, which might also have been possible to determine sex, even in videos where sexual characteristics were not evident. When sex could not be determined, the individual was classified as ND.

2.3. Time budget and ethogram

A comprehensive dataset encompassing Eurasian beaver behaviours, specific to the Mediterranean region, has been compiled (Table 1), largely following descriptions provided by Bau (2001), with only minor modifications. To categorise play behaviour, the Burghardt (2005) theoretical framework was applied. Particularly, play was defined on five key criteria. Play behaviour, whether involving direct physical contact between individuals or not, is non-functional or only partially functional within its context. It is spontaneous, occurring without

Table 1
Behavioural repertoire of the Eurasian beaver, with relevant reference. Acronyms of each behaviour are shown in brackets.

Behaviour type	Reference	Description
Allogrooming (AG)	Bau (2001)	Mutual grooming between individuals, with individuals engaging in mutual physical contact such as the use of mouth and paws to care for the other individual fur.
Avoiding obstacles (AO)	Viviano et al. (2025)	Adjusting movements during locomotion to avoid objects or obstacles.
Biting/pawing off grass (BP)	Bau (2001)	Chewing or scratching grass for feeding.
Carrying objects (CO)	Bau (2001), readapted	Transporting objects in mouth from one place to another.
Dancing (DA)	Bau (2001)	Sequence of body movements, starting with the head and gradually extending to the rest of the body, resembling a shaking motion. The movement is exaggerated, with the head rotating in circular motions.
Diving (DI)	Bau (2001)	Immersing in water with a downward motion.
Gathering of mud (GM)	Bau (2001)	Collecting mud from the bottom of the pond and carrying it on the lodge or on the dam.
Entering water (EW)	Bau (2001)	Immersion in water.
Exiting water (EX)	Bau (2001)	Leaving the water after swimming or immersion.
Exploring (EXP)	Bau (2001), readapted	Investigating the surrounding environment, sniffing in proximity to objects or places.
Foraging (FO)	Bau (2001)	Foraging on land, mostly on trunks (also including gnawing and chewing), grasses and fruits.
Nose touching (NT)	Bau (2001)	Contact with other individuals using the nose.
Pawing with front legs (PA)	Bau (2001)	Scratching the soil with front feet, without releasing any secretion.
Parental care (PC)	Bau (2001)	Behavioural patterns associated with caring for offspring or young.
Placing (PLC)	Bau (2001)	Placing a branch, mud or grass on dams and lodges.
Playing (PLY)	Bau (2001), readapted	Engaging in playful activities, including play fighting (i.e., with direct inter-individual contacts) diving drills, chasing and ambushing (i.e., without direct inter-individual contacts).
Resting (RE)	Viviano et al. (2025)	Standing still, or sitting.
Running (RU)	Viviano et al. (2025)	Moving quickly on land.
Scent marking (SM)	Bau (2001)	Marking territory using odour secretions by rubbing anal glands.
Self-grooming (SG)	Bau (2001)	Personal care through cleaning, grooming and scratching oneself by rubbing fur with mouth and paws.
Swimming (SW)	Bau (2001)	Moving through water.
Swimming and carrying (SC)	Bau (2001)	Swimming and carrying branches of grass and/or mud, collected upstream from ponds or from grass fields.
Vigilance (VI)	Bau (2001)	Being alert and attentive to potential threats or changes in the environment, by raising and moving the head laterally.
Vocalisation (VO)	Bau (2001)	Emission of a sound towards conspecifics.

external *stimuli*, and is performed for enjoyment or intrinsic satisfaction. Additionally, play is repetitive but not stereotyped and is exhibited in the absence of stress (Burghardt, 2005; Palagi and Pellis, 2023). When documenting play and other behaviours, individuals were considered "in proximity" if they were closer than the length of a single beaver body (i.e., less than 1.5 m) Each behavioural event was attributed to the observed individual age class and sex whenever possible. For each behaviour, the number of observed occurrences (defined as the time spent by the same individual in the same behaviour) and the proportion of the total observation time spent engaging in it by each age class were recorded. Every recorded behavioural event was logged in a dataset, with each row representing an observed behaviour of an individual (or interacting individuals). The dataset includes detailed information such as event duration, behaviour type, date, and time of occurrence.

Behavioural patterns were recorded in the order they were exhibited. This method provided information on the time spent in each activity, along with the observed behavioural patterns. Videos were analyzed independently by two operators (AV and EM) following a common training. The inter-rater agreement was measured through the Cohen's kappa (K: Cohen, 1960, 1968) and substantial agreements for all behaviours were obtained (K = 0.62–0.77: Landis and Koch, 1977). To ensure the reliability of the applied method, discrepancies between their analyses were compared, and in cases of disagreement, the videos were reanalyzed by both authors together to reach a consensus. Each behaviour was then carefully timed to obtain its precise duration in every video.

The behaviour of Eurasian beavers recorded in a dummy dataset was analysed using a binary coding system (0 for non-observed, 1 for observed), to indicate which behaviours were exhibited in each analysed video, for each individual. The dataset was first cleaned to ensure that all categorical variables, i.e. 'age class' (adult, subadult, kit), 'sex' (female or male, applicable only to adults), and 'season', were correctly encoded. Observations with missing values for 'sex' or 'age class' were excluded from the analysis.

The dataset was then filtered to include only observed behaviours (value = 1), and the total duration of each behaviour was summed.

Subsequently, data were analysed by season (spring, summer, autumn and winter), generating graphs to visualise seasonal activity budgets. Additionally, variation by sex and age class was examined, constructing radar bar charts for each category. The dataset was filtered to retain only relevant rows and columns for the selected variable, and the total duration of each behaviour was computed. Data were then reformatted into a long structure, where missing behaviours were assigned a value of 0. The total activity budget was again normalised as a percentage of the total observation time, and a radar chart was produced to illustrate the distribution.

To assess the influence of sex, age and periods (i.e., cold period: September-February; warm period: March-August, based on local environmental temperatures: Mori et al., 2022a) (independent variables) on behavioural duration proportions (dependent variable), generalised linear mixed models (GLMMs) with a binomial error distribution (Zuur et al., 2007) were employed, using the R package *lme4* (Bates et al., 2015). Mixed generalised linear models (GLMM) were approached with an adaptive strategy to GLMs (binomial) due to the structure of the data. Within the models, age, period, and sex were accounted as fixed terms and the river as a random factor. Separate models were fitted for 'sex', 'age class', and 'period'.

Due to the issues of model singularity and convergence problems observed in the GLMMs, which indicated limited variability between rivers, generalised linear models (GLMs) were instead ran with age, period, and sex as separate predictors. The adequacy of the GLMs was assessed using the *DHARMa* package in R, which implements a simulation-based approach for residual diagnostics of regression models. For each behavioural variable, model fit was evaluated through several diagnostic tests, e.g. i) Kolmogorov-Smirnov (KS) test for overall uniformity of residuals; ii) outlier detection test to identify influential data points; iii) dispersion test to assess whether the variance in the data matched the model's assumptions; iv) zero-inflation test to determine if the models correctly predicted the number of zeros in the data, v) Levene's test for homogeneity of variance, vi) QQ plots for visual assessment of residual distribution. A value of $p < 0.05$ was considered as the threshold for statistical significance in all diagnostic tests.

In the GLM, it has not been possible to conduct a season-specific analysis due to limited model convergence, resulting from the small sample size available for some seasons. To address this limitation, a

simplified classification into two broader thermal periods was adopted, defined as cold and warm periods (Mori et al., 2022a), grouped under the variable "period". Such an approach was necessary to ensure sufficient statistical power, as the limited number of observations per individual season compromised the model ability to detect statistically significant patterns.

To identify key behavioural drivers, the significance of specific variable levels and the Nagelkerke pseudo R^2 were computed (Nagelkerke, 1991). The analysis focused exclusively on behaviours that showed statistically significant effects of the tested levels compared to the intercept. Post-hoc pairwise comparisons were conducted using the Tukey test through the *emmeans* package (Lenth, 2024), to determine significant differences between levels of the "age" categorical variable. The estimated parameters for each behaviour, expressed as log-odds (coefficients), were analyzed to determine the likelihood of observing specific behaviours across age groups. A positive coefficient suggests a higher probability of observing the behaviour in the respective age group. Sex was determined for too few individuals to support specific analyses. To determine the independent variable which most significantly influences behaviour, a statistical comparison was made between GLM models which shared common dependent variables. Model comparison was based on Akaike's Information Criterion (AIC), and the strength of evidence supporting one model over the other was quantified using the ΔAIC, which represents the difference between the AIC values of two competing models. Following Burnham and Anderson (2002), ΔAIC values were interpreted as it follows: $\Delta AIC > 10$ indicates very strong evidence, $4 < \Delta AIC \leq 10$ substantial evidence, $2 < \Delta AIC \leq 4$ moderate evidence, and $\Delta AIC < 2$ weak or negligible support for either model. Different phases of data collection and analysis are summarised in Figure S1 in Supplementary Material 1.

3. Results

The overall dataset including 24 behaviours was filled (Table 1; Figure S2 in Supplementary Material 1; Supplementary Material 2).

3.1. Activity budget per age class

The analysis of behavioural patterns across different age classes revealed clear differences (Fig. 2a-c). Juveniles and subadults exhibited the highest levels of exploratory behaviour, with exploration accounting for a significant portion of their activity budgets (Fig. 2a-b). Dancing was also more prominent in these younger age individuals, especially among subadults. Juveniles showed a notable amount of swimming and foraging but engaged less in complex social behaviours. Adults, by contrast, displayed a broader behavioural repertoire. They engaged extensively in swimming, foraging, and carrying on land, activities that are likely linked to resource acquisition and environmental interaction. Adults also exhibited higher frequencies of self-grooming and vigilance compared to younger age individuals. Behaviours, such as placing, scent marking, and biting/pawing off grass, swimming and swimming while carrying objects were more common in adults, indicating the emergence of social and territorial behaviours with age.

Models revealed no significant differences in swimming behaviour

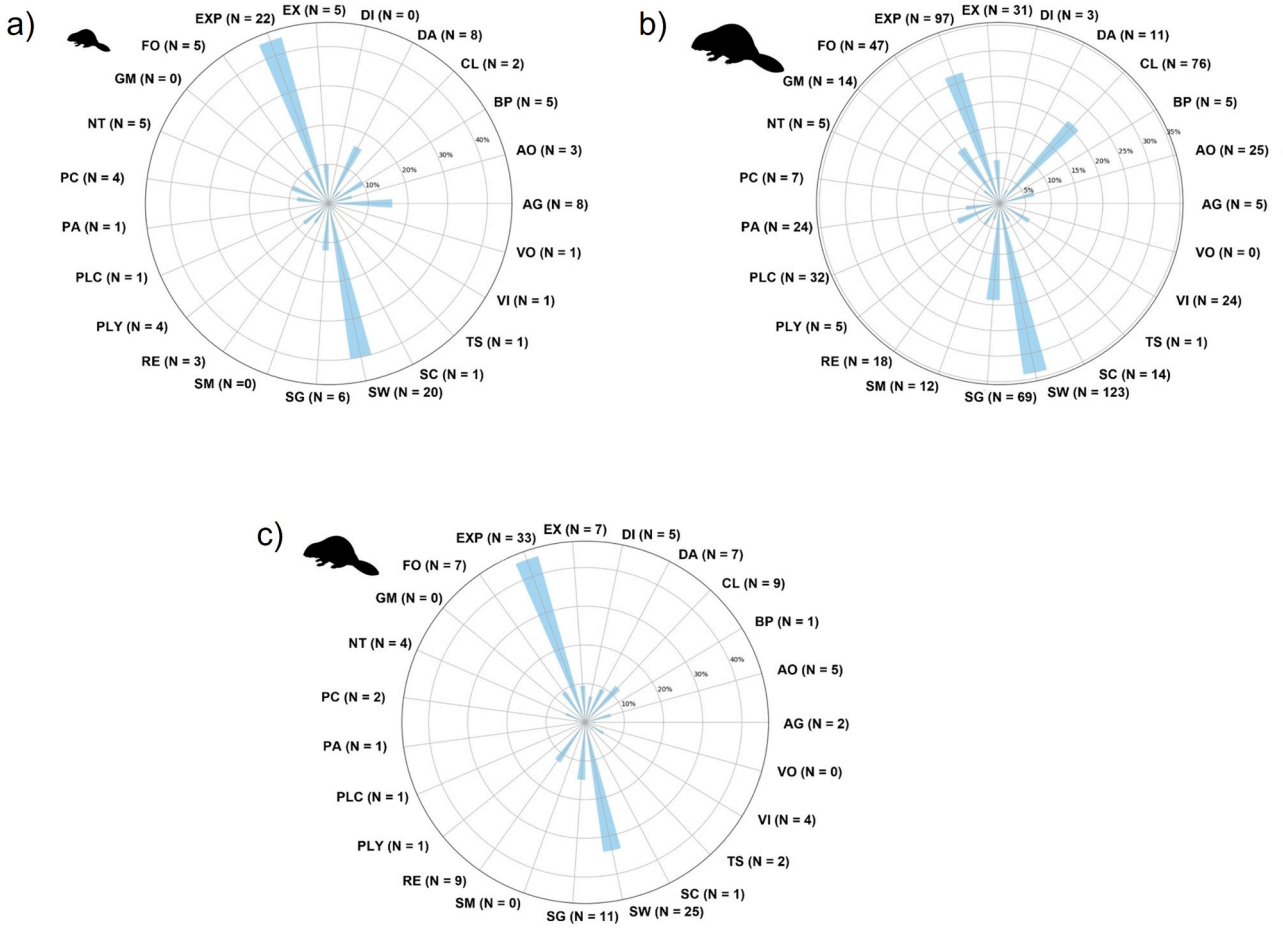

Fig. 2. Radar chart plots of beaver behaviour patterns per age classes (N tot = 498): a) kits, b) subadults, c) adults. Peaks show differences across age classes, as reported in the main text. BP, biting/pawing off grass; AO, avoiding obstacles; AG, allogrooming; VO, vocalisation; VI, vigilance; TS, tail slapping; SC, swimming and carrying; SW, swimming; SG, self-grooming; SM, scent marking; RE, resting; PLY, playing; PLC, placing; PA, pawing with front legs; PC; parental cares; NT, nose touching; GM, gathering of mud; FO, foraging; EXP, exploring; EX, exiting; DI, diving; DA, dancing; CL, carrying on land.

across age groups, indicating that adults, subadults, and juveniles exhibited similar swimming frequencies. In terms of social behaviours, juveniles showed a significantly higher propensity to engage in behaviours such as allogrooming, biting/pawing off grass, parental care, and playing compared to adults. Conversely, subadults exhibited increased levels of exploration and diving, suggesting a progression towards more autonomous behaviour. Both subadults and juveniles displayed similar tendencies for dancing and nose-touching, indicating a shared inclination for these social interactions (Table S1 in Supplementary Material 1). Differences in Nagelkerke's R^2 values were observed, providing insight into the strength of the relationship between age and the behavioural patterns. For instance, behaviours such as allogrooming (Nagelkerke $R^2 = 0.155$) and nose-touching (Nagelkerke $R^2 = 0.093$) exhibited moderate R^2 values, indicating a stronger relationship with age, particularly in juveniles. In contrast, behaviours like diving (Nagelkerke $R^2 = 0.136$) in subadults demonstrated moderate R^2 values, suggesting a moderate influence of age on these behaviours. Other behaviours, such as carrying on land, displayed smaller R^2 values (Nagelkerke $R^2 = 0.044$), reflecting a weaker association with age (Table S1 in Supplementary Material 1). The statistical analysis of contrasts between age classes revealed significant differences in several behaviours. Comparisons between adults, subadults, and juveniles showed that juveniles exhibited significantly more allogrooming than adults ($p < 0.001$), suggesting the heightened importance of this behaviour during the early stages of development, when juveniles establish social bonds. Juveniles were also significantly more inclined than adults ($p = 0.004$) to engage in biting and pawing off grass, likely as part of their tactile exploration and food learning processes. Additionally, dancing was significantly more frequent in juveniles and subadults than in adults, with juveniles particularly displaying higher frequencies ($p = 0.001$), suggesting that dancing is related to play and motor learning, behavioural patterns that predominate in the early stages of development. Juveniles showed significantly more nose-touching compared to adults ($p = 0.0045$), indicating that affiliative and social recognition are particularly pronounced in the early stages of life. Playing was also significantly more frequent in juveniles than in adults ($p = 0.023$), reinforcing the critical role of play in the physical and social development of young beavers. Both subadults and juveniles exhibited significantly more exploratory behaviour than adults ($p = 0.006$ for subadults, $p < 0.05$ for juveniles), highlighting an increased curiosity and desire to explore during the juvenile stages of development. Regarding diving, subadults demonstrated a significantly higher probability of diving compared to adults ($p = 0.001$). Data for juveniles exhibited high variability, suggesting either a lower inclination to engage in this behaviour or limitations in the available data for juveniles. Finally, adults exhibited significantly more material-carrying on land compared to juveniles ($p = 0.02$). This activity was more frequent in adults, reflecting the importance of this skill in the construction and maintenance of burrows and dams, tasks that require both experience and physical strength.

In summary, juveniles displayed a greater inclination towards social and developmental behaviour, such as allogrooming, play, physical contact, and exploration. In contrast, adults were more involved in functional activities, such as material transport on land, which are essential for the construction and maintenance of dams and burrows. Subadults, on the other hand, exhibited a shift towards a more independent behaviour, including exploration and diving (Table S2 in Supplementary Material 1).

3.2. Activity budget per sex

Due to the difficulties in sex determination, possible mainly during the lactation period, the greatest number of behaviours were only determined for the female sex (Fig. 3a). The main behaviours found in females were exploring, self-grooming and swimming (associated with exiting: Fig. 3a-b).

3.3. Activity budget per season

Across the four seasons, a detailed analysis of behavioural patterns in beavers revealed variation in activity frequencies. In spring (Fig. 4a), the most frequently observed behaviours included swimming, exploring, and foraging. Other notable activities were self-grooming, resting, and a number of less common behaviours such as dancing, tail slapping, and social interactions including allogrooming, nose touching and parental care. In summer (Fig. 4b), the exploration behaviour remained the predominant one, whereas carrying on land exhibited a significant increase. Conversely, swimming, self-grooming and foraging observations exhibited a decline in frequency when compared to spring. Allogrooming and parental care were not recorded in summer. Conversely, the avoidance of obstacles and the enhancement of vigilance observation exhibited a marked increase during the summer. In autumn (Fig. 4c), swimming peaked again, while exploring, carrying on land, and placing were also frequent. A broader diversity of behaviours was observed, including gathering of mud, biting/pawing off grass, and vigilance. Social behaviours such as allogrooming, nose touching and parental care were present but poorly represented. In winter, only swimming,

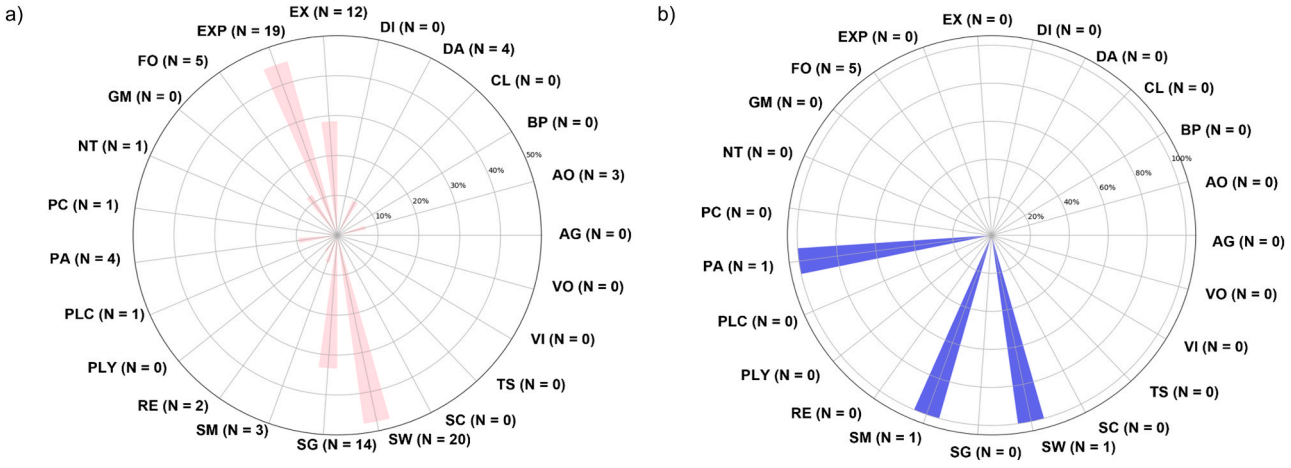

Fig. 3. Radar chart plots of beaver behaviour patterns per sex (N tot = 42): a) females in pink, b) males in blue. Peaks show differences across age classes, as reported in the main text. BP, biting/pawing off grass; AO, avoiding obstacles; AG, allogrooming; VO, vocalisation; VI, vigilance; TS, tail slapping; SC, swimming and carrying; SW, swimming; SG, self-grooming; SM, scent marking; RE, resting; PLY, playing; PLC, placing; PA, pawing with front legs; PC; parental cares; NT, nose touching; GM, gathering of mud; FO, foraging; EXP, exploring; EX, exiting; DI, diving; DA, dancing; CL, carrying on land.

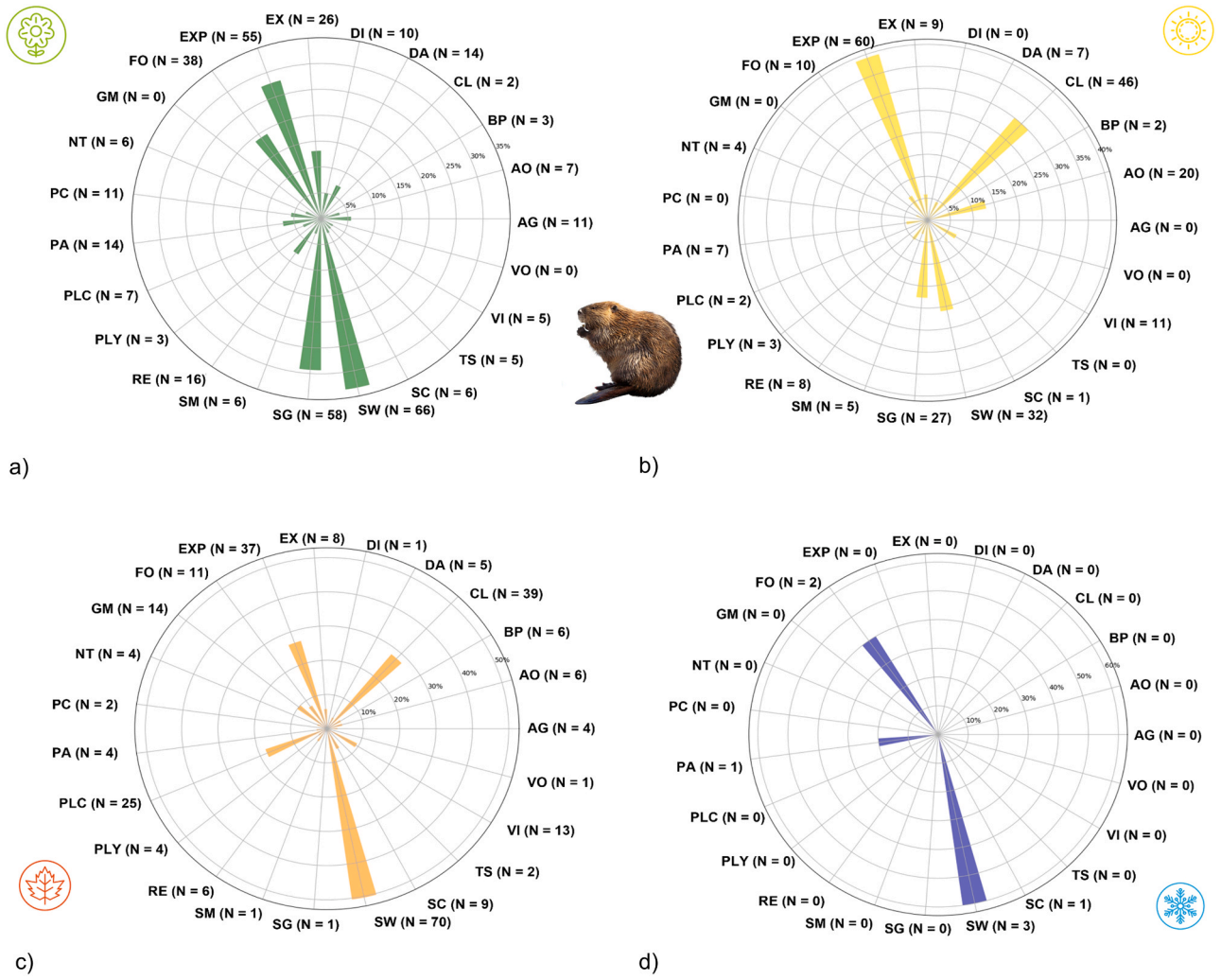

Fig. 4. Radar chart plots of beaver behaviour patterns per season (N tot = 498): a) spring in green, b) summer in yellow, c) autumn in orange, and d) winter in blue. Peaks show differences across age classes, as reported in the main text. BP, biting/pawing off grass; AO, avoiding obstacles; AG, allogrooming; VO, vocalisation; VI, vigilance; TS, tail slapping; SC, swimming and carrying; SW, swimming; SG, self-grooming; SM, scent marking; RE, resting; PLY, playing; PLC, placing; PA, pawing with front legs; PC; parental cares; NT, nose touching; GM, gathering of mud; FO, foraging; EXP, exploring; EX, exiting; DI, diving; DA, dancing; CL, carrying on land.

foraging and pawing with front legs were observed (Fig. 4d).

Models revealed a significant influence of ambient temperature (i.e., of warm and cold periods) on beaver behaviour, highlighting distinct patterns. Among the behaviours that showed statistically significant differences between periods, swimming behaviour showed a marked reduction during the warm period, as indicated by the significantly negative coefficient associated with warm conditions ($\beta = -0.988$, $p < 0.001$), with a Nagelkerke's R^2 of 0.063. Similarly, swimming while carrying materials (swimming and carrying) also declined significantly in the warm period ($\beta = -1.195$, $p = 0.02$), albeit with a more moderate effect (Nagelkerke's $R^2 = 0.043$). A comparable pattern was observed in construction-related behaviour. The placing of materials exhibited the most pronounced decrease in winter and early spring among all analyzed behaviours ($\beta = -2.086$, $p < 0.001$, Nagelkerke's $R^2 = 0.155$), indicating a substantial period effect. Likewise, terrestrial material transport (carrying on land) decreased significantly during warm months ($\beta = -0.862$, $p < 0.001$), with a moderate effect size (Nagelkerke's $R^2 = 0.040$). In stark contrast to these functional behaviours, self-grooming increased sharply during the warm period ($\beta = 3.811$, $p < 0.001$, Nagelkerke's R^2 of 0.177), suggesting that it is the most temperature-dependent (i.e., related to differences in "period") behaviour analyzed (Table S3 in Supplementary Material 1). All contrasts are statistically significant, with p-values < 0.05, confirming the behavioural differences between the cold and the warm periods (Table S4 in Supplementary Material 1).

3.4. Drivers of behavioural patterns

The diagnostic tests revealed that all models adequately fit the data, with no significant deviation in any of the assessed parameters. The Kolmogorov-Smirnov tests for all behavioural variables showed p-values ranging from 0.25 to 0.79, well above the conventional significance threshold ($p < 0.05$), indicating that residuals did not significantly deviate from the expected distribution. No significant outlier was detected in any of the models (all outlier tests, $p = 1.0$). Dispersion tests showed p-values ranging from 0.84 to 1.0, indicating no evidence of over- or under-dispersion in the data. Additionally, zero-inflation tests yielded p-values ranging from 0.976 to 1.0, confirming that the models appropriately accounted for the frequency of zero observations. Levene's tests were non-significant for all variables, confirming homogeneity of variance across groups.

Visual inspection of QQ plots further supported these findings, with residuals closely following the expected theoretical distribution in all cases. Within-group uniformity tests revealed no deviations from expectations, confirming the appropriateness of our model structure.

3.5. Model comparison

Several behaviours showed a strong preference for the age-based model (ΔAIC > 10), indicating that the ontogenetic stage is a dominant predictor. Allogrooming (ΔAIC = 17.04) and dancing behaviour (ΔAIC = 11.45) showed strong age effects. In diving (ΔAIC = 29.60), subadults were significantly more active (p = 0.0035), whereas the seasonal period did not reach statistical significance (p = 0.176). Exploratory behaviour followed a similar pattern (ΔAIC = 14.37), with both juveniles and subadults showing increased exploration, and no meaningful effect of period. Tail slapping, with a ΔAIC of 29.58, was also more common in subadults (p = 0.060, marginal), while unaffected by period (p = 0.98).

In contrast, other behaviours were best explained by the seasonal period. Self-grooming emerged as the most strongly period-driven behaviour (ΔAIC = 52.89) with no detectable effect of age. Placing behaviour also showed a substantial period effect (ΔAIC = 22.54), with a marked decline in frequency during the warm period; age had no significant effect, although a marginal trend was observed in subadults. Swimming was more frequent in the cold period (ΔAIC = 14.17), and similarly unaffected by age. Gathering of mud favored the period model (ΔAIC = 28.91), with indications of behavioural suppression during the warm period, though accompanied by high variability in estimates.

Several behaviours showed support for the age-based model (ΔAIC between 4 and 10). Biting/Pawing at grass (ΔAIC = 4.26) was significantly more frequent in juveniles, with a non-significant tendency toward reduction in the warm period (p = 0.071). Foraging (ΔAIC = 6.92) favored the age model despite a lack of significant coefficients in either model, suggesting unexplained age-related variability. Nose touching (ΔAIC = 8.93) was significantly more frequent in juveniles and subadults, with no effect of period. Moderate support (ΔAIC between 2 and 4) was found for playing (ΔAIC = 3.91), with juveniles exhibiting significantly higher frequencies, and no period effect. Pawing with front legs (ΔAIC = 3.32) and scent marking (ΔAIC = 2.40) showed preference for the age model, though without statistically significant terms.

Moderate support for period-based models was observed in avoiding obstacles (ΔAIC = 2.98), exiting (ΔAIC = 3.03), and vigilance (ΔAIC = 2.32). While no predictors were statistically significant, vigilance showed a near-significant decrease during the warm period, with age having no detectable effect.

A subset of behaviours yielded ΔAIC values below 2, suggesting minimal explanatory difference between age and period models. Carrying on land (ΔAIC = 2.09) showed decreases both during the warm period and in juveniles, yet the overall model comparison indicated near-equivalence. Parental care (ΔAIC = 1.45) was more frequent in juveniles, while resting (ΔAIC = 2.36) was more common among subadults. Vocalisations (ΔAIC = 0.09) presented virtually identical model fits, with high variability and large standard errors suggesting behavioural rarity or context dependency. A clear dichotomy emerges from the model selection results. Behaviours related to social development, including allogrooming, dancing, diving, exploring, tail slapping, and nose touching, are best explained by the ontogenetic stage, consistent with their known developmental functions. In contrast, behaviours likely linked to ecological constraints or environmental responsiveness, such as self-grooming, placing, swimming, and mud gathering, exhibit strong seasonal period modulation, indicating adaptive behavioural shifts across temperature regimes. Behaviours with low ΔAIC values likely reflect a mixed influence of age and environment or involve additional, unmeasured predictors. Notably, the extremely high ΔAIC for self-grooming and tail slapping emphasises how some behaviours are almost exclusively governed by a single factor, underscoring the utility of ΔAIC in revealing behavioural architecture (Table S5 in Supplementary Material 1).

4. Discussion

This work reports the first ethological assessment – including both behavioural repertoire and yearly activity budget – of the Eurasian beaver in a natural setting in southern Europe. Results showed that age significantly influences the behavioural repertoire of Eurasian beavers, consistent with findings in other large rodents (Viviano et al., 2025). Specifically, most videos occurred in nighttime, supporting our prediction (i). The exploratory behaviour and play observed in juveniles and subadults align with established ethological principles (Iki, 2025), as these behaviours are the building-blocks for the development of the environment orientation, motor skills, and the assessment and establishment of social relationships (Schneider and Koch, 2005; Gromov, 2017). The increased frequency of allogrooming and nose-touching among adult beavers interacting with younger individuals further supports the importance of social development during early life stages (Viviano et al., 2025).

Conversely, adult beavers exhibited a higher prevalence of swimming, foraging, and carrying behaviours, reflecting their roles in resource acquisition, territory maintenance, and dam construction, indicating the emergence of social and territorial behaviours with age (Żurowski, 1992). These activities are energetically demanding and require both experience and physical maturity, thus explaining their increased occurrence in adults (Ronnquist and Westbrook, 2021).

A marked influence of seasonality on beaver behaviour was also observed, most likely in relation to thermoregulation and resource management (Dyck and MacArthur, 1992), which was not detected in northern Europe (Sharpe and Rosell, 2003). Swimming activity increased during the cold period as a possible way to generate heat through physical exertion, thereby aiding in thermoregulation (MacArthur, 1989). Additionally, swimming may facilitate the maintenance and monitoring of underwater structures, which are crucial for shelter and insulation during winter (Larsen et al., 2021). In summer, swimming or aquatic behaviours may decrease in frequency, as rivers in Italy, a Mediterranean region, often experience hydrological deficits (Mori et al., 2022c), potentially increasing beaver exposure to predators due to reduced water availability and cover. The concurrent increase in carrying and placing materials during the cold period supports the hypothesis that dam and lodge maintenance is critical for creating a stable microclimate (Dyck and MacArthu, 1993; Rosell and Campbell-Palmer, 2022). These structures provide protection from predators and mitigate harsh environmental conditions, thereby enhancing the beaver survival perspectives (Wilson, Bremner-Harrison, 2025). Accordingly, material placement showed the strongest seasonal effect, reflecting a heightened investment in construction activities aimed at maintaining and reinforcing dams and lodges, structures essential for ensuring a stable microclimate. Similarly, the increase in terrestrial transport in the cold period corresponds with increased material collection for construction and potential food storage. In contrast, self-grooming behaviour significantly increased during the warm period, suggesting a shift in energy allocation (Patenaude and Bovet, 1984).

Overall, beaver behaviours related to social development, such as allogrooming, dancing, and exploration, are predominantly age-driven, highlighting the importance of ontogenetic factors in shaping these activities. Conversely, behaviours linked to ecological constraints, such as swimming, placing, and self-grooming, are strongly influenced by seasonal variation, reflecting adaptive responses to environmental conditions.

The behavioural plasticity observed in Eurasian beavers underscores their adaptability to diverse environmental conditions, which is crucial for their success in recolonising areas and establishing populations in new habitats (Halley et al., 2021). The role of the Eurasian beaver as an ecosystem engineer is further emphasised by the seasonal modulation of construction-related behaviour, which directly alters the structure and function of aquatic and riparian ecosystems (Brazier et al., 2021).

From an evolutionary perspective, this study highlights the

interactions between ontogenetic and environmental factors in shaping behavioural traits. The age-related differences may reflect selective pressures promoting a proper social development in juvenile individuals and reproductive success and survival in adults. The seasonal variations show the adaptive value of behavioural flexibility in response to changing environmental demands. Furthermore, beavers proactively modify their habitat in response to seasonal changes (prediction ii). Annual data from northern Europe are needed to confirm whether the behavioural plasticity of this species reflects an adaptive strategy to local environmental conditions.

The behavioural repertoire of Eurasian beavers in central Italy partly differs from that described in northern European populations (Bau, 2001). The most pronounced variation is observed in foraging behaviour, which constitutes the dominant behaviour in Bau (2001), whereas the frequency recorded in the current study was lower. Conversely, a greater preponderance of active swimming and on land (i.e., exploring, carrying on land, avoiding obstacles and resting) behaviours were recorded in the present study. A further discrepancy includes the higher frequency of building behaviour (i.e., placing) recorded by Bau (2001) compared to the current work. Aggressive behaviour was only recorded in Bau (2001), whereas parental cares were only observed in this work (Figure S3 in Supplementary Material 1). The occurrence of a single dam in the central Italy study area (Di Lorenzo et al., 2024) may have reduced the necessity for intensive building behaviour compared to the more established populations studied of northern Europe by Bau (2001). However, the opportunistic placement of camera traps near lodges and dens in this study may have biased observations toward affiliative behaviours (e.g., parental cares), and reduced documentation of building activities. Additionally, ecological differences such as habitat structure, food availability, and the limited number of dams in central Italy may also contribute to the observed behavioural variations. Therefore, while also population density may play a role, collected data in central Italy suggest that both local environmental factors are important factors potentially shaping the behavioural repertoire of Eurasian beavers in this region. Further research is needed to more accurately assess behavioural differences between male and female beavers, given that only a limited number of individuals were sexually identified in this study (e.g., see Sharpe and Rosell, 2003).

To conclude, this study provides novel and detailed insights into the behavioural ecology of Eurasian beavers in central Italy. Differences with northern Europe are likely influenced by both ecological factors and methodological aspects, including the opportunistic placement of camera traps near lodges and dens, which may have biased observations toward some behaviours (e.g., tree-felling, building behaviour: Rosell and Campbell-Palmer, 2022). Despite these limitations, the study contributes valuable baseline data for a region where beaver populations are poorly known and highlights the behavioural plasticity of the species in response to local environmental conditions. The results underscore the importance of long-term and systematic behavioural monitoring to assess ecological impacts, particularly in relation to habitat modification, population expansion, and interactions with human communities. Future research should expand the comparative assessment of beaver behavioural repertoires across biogeographical regions, addressing current gaps in the literature and the methodological challenges of obtaining comprehensive, non-invasive behavioural data in semi-aquatic species, which are essential for improving ecological understanding and evidence-based management (e.g., Viviano et al., 2025).

CRediT authorship contribution statement

Andrea Viviano: Validation, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Leonardo Ancillotto:** Writing – original draft, Visualization, Validation, Supervision, Funding acquisition, Data curation. **Elisabetta Palagi:** Visualization, Validation, Supervision, Software, Resources, Methodology. **Olivia Dondina:** Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Formal analysis. **Emiliano Mori:** Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Data curation, Conceptualization. **Norma Lelli:** Writing – review & editing, Visualization, Supervision.

Ethics statement

This study did not involve the manipulation of living animals. We relied solely on passive camera traps, which do not disturb wildlife.

Conflict of interest statement

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2026.105363.

Data availability statement

All used data are available as Supplementary Materials 1 and 2.

References

Bartra Cabre, L., Mayer, M., Steyaert, S., Rosell, F., 2020. Beaver (*Castor fiber*) activity and spatial movement in response to light and weather conditions. Mammal. Biol. 100, 261–271. https://doi.org/10.1007/s42991-020-00029-7.

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

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

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human–wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.01.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., Brown, C.M., 2021. Beaver: nature's ecosystem engineers. Wiley Interdiscip. Rev. Water 8, e1494. https://doi.org/10.1002/wat2.1494.

Burghardt, G., 2005. Defining and recognizing play. In: Pellegrini, A.D. (Ed.), The Oxford Handbook of the Development of Play. Oxford University Press, New York, USA, pp. 9–18.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, Second ed. Springer Editions, Berlin Heidelberg.

Cohen, J., 1960. A coefficient of agreement for nominal scales. Ed. Psychol. Meas. 20, 37–46.

Cohen, J., 1968. Weighted kappa: nominal scale agreement with provision for scaled disagreement or partial credit. Psychol. Bull. 70, 213–220.

Cosma, R., 2001. Biometria E Determinazione Dell'età Nell'istrice. Msc Thesis in Scienze Biologiche. Università degli Studi di Siena, Siena, Italy.

Danilov, P.I., Kanshiev, V.Y., 1983. The state of populations and ecological characteristics of European (*Castor fiber* L.) and Canadian (*Castor canadensis* Kuhl.) beavers in the north western USSR. Acta Zool. Fenn. 174, 95–97.

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. https://doi.org/10.1007/s13364-019-00443-4.

Di Lorenzo, T., Tabilio Di Camillo, A., Mori, E., Viviano, A., Mazza, G., Pontalti, A., Rogora, M., Fiasca, B., Di Cicco, M., Galassi, D.M.P., 2024. Effects of a beaver dam on the benthic copepod assemblage of a Mediterranean river. Sci. Rep. 14, 8956. https://doi.org/10.1038/s41598-024-59456-y.

Dyck, A.P., MacArthu, R.-A., 1993. Seasonal variation in the microclimate and gas composition of beaver lodges in a boreal environment. J. Mammal. 74, 180–188.

Dyck, A.P., MacArthur, R.A., 1992. Seasonal patterns of body temperature and activity in free-ranging beaver (*Castor canadensis*). Can. J. Zool. 70, 1668–1672.

Dytkowicz, M., Hinds, R., Megill, W.M., Buttschardt, T.K., Rosell, F., 2023. A camera trapping method for the targeted capture of Eurasian beaver (*Castor fiber*) tails for individual scale pattern recognition. Eur. J. Wildl. Res. 69, 39. https://doi.org/10.1007/s10344-023-01654-6.

Falaschi, M., Ficetola, G.F., Viviano, A., Mazza, G., Mori, E., 2024. Environmental suitability and potential range expansion of the Eurasian beaver in Italy. Anim. Conserv. 27, 324–337. https://doi.org/10.1111/acv.12910.

Gallant, D., Léger, L., Tremblay, É., Berteaux, D., Lecomte, N., Vasseur, L., 2016. Linking time budgets to habitat quality suggests that beavers (*Castor canadensis*) are energy maximizers. Can. J. Zool. 94, 671–676.

Greggor, A.L., Blumstein, D.T., Wong, B., Berger-Tal, O., 2019. Using animal behavior in conservation management: a series of systematic reviews and maps. Environ. Evid. 8, 23. https://doi.org/10.1186/s13750-019-0164-4.

Gromov, V.S., 2017. The evolution of sociality in rodents: a family affair. Russ. J. Theriol. 16, 47–65. https://doi.org/10.15298/rusjtheriol.16.1.05.

Halley, D.J., Saveljev, A.P., Rosell, F., 2021. Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. Mammal. Rev. 51, 1–24. https://doi.org/10.1111/mam.12216.

Herr, A., Rosell, F., 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). J. Zool. 262 (4), 439–446. https://doi.org/10.1017/S0952836904005481.

Hinds, R., Dytkowicz, M., Tania, M., Megill, W.M., Rosell, F., 2023. A tale of tails: The use of Eurasian beaver (*Castor fiber*) tails for ageing and individual identification. Eur. J. Wildl. Res. 69, 88. https://doi.org/10.1007/s10344-023-01718-7.

Hodgdon, H.E., Larson, L.S., 1973. Some sexual differences in behaviour within a colony of marked beavers (*Castor canadensis*). Anim. Behav. 21, 147–152. https://doi.org/10.1016/S0003-3472(73)80052-1.

Iki, S., 2025. From curiosity to play: re-evaluating the evolutionary origins of play. Biol. Rev. 100, 1467–1483. https://doi.org/10.1111/brv.70009.

Landis, J.R., Koch, G.G., 1977. An application of hierarchical kappa-type statistics in the assessment of majority agreement among multiple observers. Biometrics 33, 363–374. https://doi.org/10.1111/brv.70009.

LaPoint, S., Gallery, P., Wikelski, M., Kays, R., 2013. Animal behaviour, cost-based corridor models, and real corridors. Landsc. Ecol. 28, 1615–1630. https://doi.org/10.1007/s10980-013-9910-0.

Larsen, A., Larsen, J.R., Lane, S.N., 2021. Dam builders and their works: beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. EarthSci. Rev. 218, 103623. https://doi.org/10.1016/j.earscirev.2021.103623.

Lenth, R.V. 2024. emmeans: Estimated Marginal Means, aka Least–Squares Means. Available at: ⟨https://CRAN.R-project.org/package=emmeans⟩. Accessed on 27.01.2025.

MacArthur, R.A., 1989. Energy metabolism and thermoregulation of beaver (*Castor canadensis*). Can. J. Zool. 67, 651–657.

Mikulka, O., Homolka, M., Drimaj, J., Kamler, J., 2020. European beaver (*Castor fiber*) in open agricultural landscapes: crop grazing and the potential for economic damage. Eur. J. Wildl. Res. 66, 1–10. https://doi.org/10.1007/s10344-020-01442-6.

Mori, E., Viviano, A., Mazza, G., Lazzeri, L., 2022b. Is the grey wolf a potential predator of Eurasian beavers in Central Italy? Gortania 44, 73–78. https://doi.org/10.57614/GORT20380402.2022.44.4.

Mori, E., Mazza, G., Pucci, C., Senserini, D., Campbell-Palmer, R., Contaldo, M., Vivia, A., 2022a. Temporal activity patterns of the Eurasian beaver and coexisting species in a Mediterranean ecosystem. Animals 12, 1961. https://doi.org/10.3390/ani12151961.

Mori, E., Viviano, A., Scarfò, M., Preti, F., Pucci, C., Ciuti, F., Giovannelli, A., Traversi, M. L., Senserini, D., Mazza, G., 2022c. Bark stripping behaviour by a large-sized rodent, the crested porcupine, as an adaptation to climate change. Biologia 77, 3525–3529. https://doi.org/10.1007/s11756-022-01243-z.

Mori, E., Puttock, A., Viviano, A., Mosini, A., Campbell-Palmer, R., Ancillotto, L., Trentanovi, G., Scarfò, M., Leoncini, F., Pontarini, R., Mazza, G., Needham, R., 2024. How much Eurasian beaver activity is there in Italy? Using field signs to monitor and map a returned species. Mammal. Res. 69, 519–532. https://doi.org/10.1007/s13364-024-00763-0.

Mori, E., Gallese, F., Ancillotto, L., 2025. Social behaviour of the crested porcupine in urban and rural areas. Acta Ethol. 28, 109–117. https://doi.org/10.1007/s10211-025-00459-x.

Mortensen, R.M., Reinhardt, S., Hjønnevåg, M.E., Wilson, R.P., Rosell, F., 2021. Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver. Anim. Biotel. 9, 1–19. https://doi.org/10.1186/s40317-021-00259-7.

Nagelkerke, N.J., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.

Nica, A., Petrea, M.S., Simionov, I.A., Antache, A., Cristea, V., 2022. Ecological impact of European Beaver, *Castor fiber*. Sci. Pap. Ser. D. Anim. Sci. 65, 640–647.

Nolet, B.A., Rosell, F., 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. Biol. Conserv. 83, 165–173. https://doi.org/10.1016/S0006-3207(97)00066-9.

Palagi, E., Pellis, S.M., 2023. Play behavior: a comparative perspective. In: Freeberg, T. M., Ridley, A.R., d'Ettorre, P. (Eds.), Routledge Handbook of Comparative Psychology. Taylor & Francis Editions, Oxford, UK, pp. 202–212.

Pașca, C., Ionescu, G., Fedorca, A., Jurj, R., Sîrbu, G., Popa, M., Gridan, A., Ionescu, O., 2022. Beaver management in Romania between challenges and perspectives. The National Action Plan for the Conservation of the Eurasian beaver population (*Castor fiber* L.) - synthesis. Rev. Silvic. Cineg. 27, 109.

Patenaude, F., Bovet, J., 1984. Self-grooming and social grooming in the North American beaver, *Castor canadensis*. Can. J. Zool. 62, 1872–1878. https://doi.org/10.1139/z84-273.

Preti, F., Saracino, R., Signorile, A.V., Dani, A., Pucci, C., Rillo Migliorini Giovannini, M., 2025. Beavers as water bioengineers: effects on the bank roughness in the early years of new settlement in Tuscany. J. Ecohydraulics 1–15. https://doi.org/10.1080/24705357.2025.2540784.

Ronnquist, A.L., Westbrook, C.J., 2021. Beaver dams: how structure, flow state, and landscape setting regulate water storage and release. Sci. Tot. Environm. 785, 147333. https://doi.org/10.1016/j.scitotenv.2021.147333.

Rosell, F., Campbell-Palmer, R., 2022. Activity patterns and life history. In: Beavers: Ecology, Behaviour, Conservation, and Management. Oxford Academic Editions, Oxford, UK, pp. 172–220. https://doi.org/10.1093/oso/9780198835042.003.0006.

Rosell, F., Bozser, O., Collen, P., Parker, H., 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal. Rev. 35, 248–276. https://doi.org/10.1111/j.1365-2907.2005.00067.x.

Schneider, M., Koch, M., 2005. Deficient social and play behavior in juvenile and adult rats after neonatal cortical lesion: effects of chronic pubertal cannabinoid treatment. Neuropsychopharmacol 30, 944–957. https://doi.org/10.1038/sj.npp.1300634.

Schramm, D.L., 1968. A field study of beaver behaviour in East Barnard. Dartmouth College, Dartmouth, UK.

Sensi, M., Mazza, G., Mori, E., Esattore, B., 2020. Valutazione ambientale del Fiume Merse (Toscana) associata a campionamenti del granchio di fiume *Potamon fluviatile*. Atti Soc. Tosc. Sci. Nat. Mem. Ser. B 127, 121–126. https://doi.org/10.2424/ASTSN.M.2020.14.

Sharpe, F., Rosell, F., 2003. Time budgets and sex differences in the Eurasian beaver. Anim. Behav. 66, 1059–1067. https://doi.org/10.1006/anbe.2003.2274.

Singh, M., Kaumanns, W., 2005. Behavioural studies: a necessity for wildlife management. Curr. Sci. 89, 1230–1236.

Stanton, L.A., Sullivan, M.S., Fazio, J.M., 2015. A standardized ethogram for the Felidae: a tool for behavioural researchers. Appl. Anim. Behav. Sci. 173, 3–16. https://doi.org/10.1016/j.applanim.2015.04.001.

Swinnen, K.R., Strubbe, D., Matthysen, E., Leirs, H., 2017. Reintroduced Eurasian beavers (*Castor fiber*): colonization and range expansion across human-dominated landscapes. Biodiv. Conserv. 26, 1863–1876. https://doi.org/10.1007/s10531-017-1333-9.

Tevis, L., 1950. Summer behaviour of a family of beavers in New York State. J. Mammal. 31, 40–65.

Viviano, A., Ancillotto, L., Dondina, O., Burchielli, A., Miccolis, D., Mori, E., 2025. 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. Appl. Anim. Behav. Sci. 284, 106534. https://doi.org/10.1016/j.applanim.2025.106534.

Viviano, A., Mazza, G., Di Lorenzo, T., Mori, E., 2022. Housed in a lodge: occurrence of animal species within Eurasian beaver constructions in Central Italy. Eur. J. Wildl. Res. 68, 75. https://doi.org/10.1007/s10344-022-01625-3.

Wilson, J.B., Bremner-Harrison, S., 2025. A systematic literature review investigating the association between biodiversity and beaver lodges. Mammal. Rev. 55, e12363. https://doi.org/10.1111/mam.12363.

Wróbel, M., Krysztofiak-Kaniewska, A., 2020. Long-term dynamics of and potential management strategies for the beaver (*Castor fiber*) population in Poland. Eur. Zool. J. 87, 116–121. https://doi.org/10.1080/24750263.2020.1727969.

Żurowski, W., 1992. Building activity of beavers. Acta Theriol. 37, 403–411.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data680Springer EditionsNew York, USA.