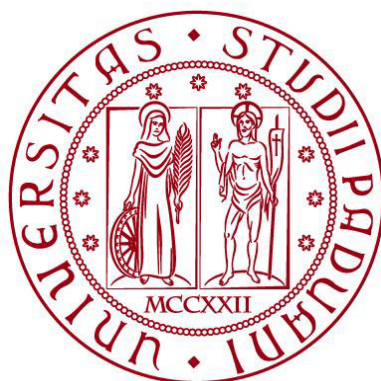


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TESI DI LAUREA

**Investigating the link between behavioural syndromes
and reproductive effort through the movement ecology
of a large mammal**

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CONTENTS

1. INTRODUCTION.....	2
1.1 Concept of animal personality	2
1.2 Pace Of Life Syndrome Hypothesis (POLS)	4
1.3 Correlations of personality traits: behavioural syndromes.....	6
1.4 Personality and movement ecology	7
1.5 Study aims, Hypothesis, and Predictions	10
2. MATERIALI E METODI.....	12
2.1 Study Area.....	12
2.2 Study Species	14
2.3 Data collection	16
2.3.1 Captures and GPS-tracking	16
2.3.2 Behavioural data from observation in the field.....	18
2.4 Statistical analysis	21
2.4.1 Movement traits calculation	21
2.4.2 Among-individual (co)variance of rut behaviour	25
2.4.3 Individual estimates and back-transformation	26
2.4.4 Among-individual axis and behavioural alignment	27
3. RESULTS	28
3.1 Among-individual variation in each trait	28
3.2 A personality / pace-of-life axis (full-posterior PCA)	31
3.3 Alignment between the axis and rut behaviour.....	34
4. DISCUSSION	35
5. BIBLIOGRAPHY	41

1. INTRODUCTION

1.1 Concept of animal personality

Inter-individual variations in behaviour represents a key target of research within animal ethology (Réale et al. 2010). In accordance with the definition proposed by Dubois et al. 2020, animal personality refers to inter-individual differences that are context dependent yet time consistent.

Personality cannot be reduced to the totality of behaviours observed in an individual but only to the fraction of behavioural variation due to differences between individuals, which is defined by repeatability (R) (Bell et al. 2009). High repeatability corresponds to low within-individual variation relative to between-individual variation. The criterion of repeatability allows personality traits to be distinguished from behavioural variations due to short-term behavioural plasticity and context-dependent responses, such as temporary internal states or environmental conditions (Dochtermann et al. 2013).

The meta-analysis by Bell et al. (2009), conducted on 98 species from 114 studies ranging from invertebrates to vertebrates, found that the repeatability of behaviour was significantly greater than zero, and that roughly 35% of the variation among individuals in behaviour could be attributed to individual differences (Bell et al. 2009). A wide variety of behavioural tendencies have been reported as significantly repeatable within individuals, including aggressiveness, boldness, activity level, cooperativeness, fearfulness, dispersal tendency, exploration tendency, docility, impulsivity, sociability, and responsiveness to environmental stimuli (Bell et al. 2009; Gosling, 2001; Réale et al. 2007; Sih et al. 2004).

However, individual differences in personality and behavioural plasticity in response to environmental conditions both contribute to the observed behavioural variation. In order to distinguish these factors, it is necessary to account for the

environment and thus control for the context when inferring consistent inter individual differences (Hertel et al. 2020; Dubois et al. 2020).

From a broader perspective, such puzzling animal personality variation is expected to have far-reaching ecological and evolutionary consequences (Dall et al. 2004; Sih et al. 2004). Several studies indeed show that differences in behaviour are often heritable (van Oers et al. 2005) and related to fitness (Dingemanse e Réale, 2005; Smith e Blumstein, 2008).

Heritability of personality traits implies that like other phenotypic traits, they can evolve by natural selection (Wolf et al. 1998).

Considering this, it is expected that over time phenotypic variation would move towards greater adaptation and that a single optimal behavioural profile would prevail. However, observational evidence shows that consistent behavioural variation persists across populations and species (Dingemanse e Réale, 2005).

One hypothesis developed to explain why the evolutionary mechanisms maintain variation of personality within populations may follow the trade-off hypothesis (Sih et al. 2004; Wolf et al. 2007) according to which individual fitness varies depending on the context in which behaviours are expressed. The personality trait of aggressiveness, for example, may be advantageous in competition with conspecifics for mates and thus lead to greater reproductive success, but may be costly if this behavioural pattern is maintained in the antipredator context, thus lowering survival (Sih et al. 2004; Stamps 2007).

A deeper analysis of these evolutionary dynamics is proposed by the Pace of Life Syndrome hypothesis (POLS) that tries to introduce the trade-off of behaviour in a wider framework, explaining the individual differences in personality from a physiological and life-history perspective.

1.2 Pace of Life Syndrome Hypothesis (POLS)

POLS expands predictions from the classic life-history theory by including behaviour and physiology into an evolutionary framework, in which individuals differ from each other in the amount of resources allocated to either survival or reproduction (Polverino et al. 2018).

Since animals generally do not have access to (or cannot process) an unlimited amount of food, the principle of allocation of energy to different functions (e.g., growth, reproduction, and maintenance) represents a central theme in evolution (Haldane 1931). This time-energetic constraint, in turn, may generate trade-offs in which the energy allocated to one function cannot increase unless that allocated to another decreases (Careau et al. 2015).

The Pace of Life Syndrome hypothesis proposes an integrative approach between the field of energetics and animal personality (Careau et al. 2012; Laskowski et al. 2022), linking “pace”, as energy expenditure, with behavioural responses. In particular, the hypothesis posits that individual differences in behaviour should be integrated with morphological, physiological, and life-history traits along a slow-to-fast pace-of-life continuum (Réale et al. 2010).

The assumption is that a “fast” profile is associated with higher levels of activity, aggressiveness, and risk-taking compared to a “slow” profile, which is linked to more conservative, conflict- and risk-avoiding individuals.

The POLS hypothesis predicts that individuals with a “slow” pace of life exhibit relatively slow growth rates, reach sexual maturity later in life, have longer lifespans, show stronger immune responses, and are expected to avoid risky situations (Royauté et al. 2018). In contrast, individuals with a “fast” pace of life are expected to adopt a “live fast–die young” strategy and are less risk-averse due to higher metabolic rates and lower stress reactivity.

A key concept in POLS is that different behavioural, physiological, and energetic traits lead to alternative solutions to the challenges of reproduction. Alternative reproductive tactics (ARTs) often align with stable inter-individual differences, so

that individuals following different tactics achieve similar fitness through distinct life-history routes (Rohr-Bender et al. 2024).

Across species, reproductive strategies can be also described along the capital-income breeding continuum. Capital breeders rely on energy reserves accumulated before the reproduction period starts, while income breeders continue to forage during the reproductive period itself, without a dramatic increase in eating activity in the previous months (Apollonio et al. 2020). Such foraging decisions represent alternative strategies for coping with reproductive costs and therefore have important consequences for an organism's fitness (Jönsson 1997). A capital-breeding strategy allows individuals to be more competitive during the mating season, but storing energy for future reproduction also entails upfront costs (e.g., an increased predation risk), which are justified only if the resulting reproductive benefits outweigh these costs (Stephens et al. 2009).

We propose that an income vs capital breeder continuum might emerge within the same species as ARTs following a distribution predicted by POLS. “Fast” profiles could be associated with a capital breeding strategy that reflects the high investment of these individuals in the proximate reproductive period. In contrast, “slow” individuals may rely more on long-term reproduction, adopting a conservative “income-breeding” reproductive strategy.

The hypothesis indeed assumes that selection has favoured correlated suites of life-history and behavioural traits to resolve the trade-off between current and future reproduction, and that behaviours help to mediate this key trade-off (Dammhahn et al. 2018).

Studies on field crickets (*Gryllus integer*) (Niemelä et al. 2012) and grey mouse lemurs (*Microcebus murinus*) (Dammhahn 2012) support that a trade-off between current and future reproduction can lead to personality variation.

For example, in the case of boldness, the general trend indicates that bolder individuals have greater reproductive success than shyer ones, particularly in males, but have shorter life spans. This last result is especially pronounced in wild

fish, guppies (*Poecilia reticulata*), in which the tendency to inspect predators has often been used as an indicator of boldness (Dugatkin e Alfieri 2003). Contrary, shy individuals may have reduced short-term reproductive success but live longer and, therefore, have the same overall fitness as bold individuals. Such a pattern is consistent with recent models proposed by Stamps (2007) and Wolf et al. (2007) explaining the evolution and maintenance of animal personalities.

Although this conceptual framework seems intuitive, relatively few formal mathematical models have examined whether and how behaviour is expected to covary with physiology and life-history traits (Wolf et al. 2007; Engqvist et al. 2015). Moreover, despite the many theoretical papers proposing the pace-of-life syndrome hypothesis as a unifying framework linking behaviour, physiology, and life-history, empirical findings for behavioural traits have been inconsistent e.g. (Careau et al. 2015; Mathot et al. 2015; Chang et al. 2024). While some studies provide strong support for the hypothesis' predictions (Careau et al. 2010), others report only partial agreement (Polverino et al. 2018).

1.3 Correlations of personality traits: behavioural syndromes

Within the same individual, specific combinations of personality traits often emerge (Stratton et al. 2023); for example, highly active individuals may also be highly aggressive, while inactive individuals exhibit low aggressive tendencies. This correlation is known as a “behavioural syndrome” (Dochtermann et al. 2013) and the identification of such syndromes has stimulated a new view of the study of animal behaviour (Sih et al. 2003, 2004). The idea is that when traits are correlated, they should be studied together, as a package, rather than as isolated units, considering animal behaviour from a multivariate rather than univariate perspective (Sih et al. 2003, 2004).

Correlations among personality traits underlying behavioural syndromes can be governed both by constraints and correlational selection (Han et al. 2019; Royauté et al. 2020; Smith et al. 2012). From the constraint perspective pleiotropic genes and shared molecular mechanisms constitute constraints and the evolution of a

behaviour will influence related ones (Dochtermann et al. 2013; Royauté et al. 2020). In an adaptive scenario, syndromes reflect alternative behavioural strategies for coping with a variable environment (Bell 2007), responding to selection pressures acting at the local level (Dingemanse et al. 2007; Michelangeli et al. 2019).

Risk-taking, activity, and exploration are behaviours that systematically recur across different species, ecological contexts, and evolutionary scales (MacKinlay et al. 2023; Collins et al. 2022). Research across taxa, from fish and birds to mammals and insects, robustly supports that risk-taking (often conceptualized as boldness) and exploratory behaviour frequently covary, forming a behavioural syndrome also in wild population (Wilson et al. 2009; Wilson et al. 2010; Garamszegi et al. 2009; Hall et al. 2015; Kelleher et al. 2018; Michelangeli et al. 2019; Hertel et al. 2019; Hughes et al. 2025). Similarly, numerous lines of evidence also demonstrate correlations between activity and exploration (Michelangeli et al. 2019; Hughes et al. 2025; Martorell-Barceló et al. 2023) and between activity and boldness (Rudin et al. 2017; Wilson et al. 2009; Martorell-Barceló et al. 2023; Miguel et al. 2024).

Several behavioural tendencies such as exploration, boldness, and activity, in addition to being often correlated, are directly linked to movement (Gharnit et al. 2020; Schirmer et al. 2019, 2020; Dhellemmes et al. 2021). Different behavioural profiles can therefore have a direct consequence on the movement ecology and movement-related traits are the personality traits which determine this correlation.

1.4 Personality and movement ecology

Within behavioural ecology, animal personality and movement ecology have mostly developed in parallel and are still poorly intertwined (Spiegel et al. 2017). However, some studies have correlated personality traits measured with classical behavioural tests with the spatial movement metrics. Several personality traits like activity, exploration, boldness or aggressiveness have been shown to have

consequences for dispersal (Dingemanse et al. 2003; Duckworth et al. 2007) or space use (Boon et al. 2008).

Some studies on free-ranging rodents indicate that bolder individuals have larger home ranges and are also more mobile and active in comparison with shy conspecifics (Gharnit et al. 2020; Schirmer et al. 2019, 2020). Another example is that of lemon sharks, *Negaprion brevirostris*, in which a correlation between explorative behaviour measured in captive conditions and their average distance from refuges once released in the wild has been found (Dhellemmes et al. 2021). Such correlations are also evident at the genetic level, with strong direct estimates reported between, for example, risk-taking and spatial exploration in great tits (Van Oers et al. 2004) and between aggression and dispersal in western bluebirds (Duckworth et al. 2009).

These findings demonstrate that differences in personality can drive individuals to systematically select for certain environmental conditions. Viewed from the reverse perspective, since movement strategies directly depend on personality, a careful analysis of space use and habitat selection patterns may allow the behavioural profile of an individual to be reconstructed.

Movement metrics such as intensity of use, residence time (Hertel et al. 2020) and time to return (Gehr et al. 2020), allow a quantitative approach to the description of movement and constitute proxies for other behavioural types. The use of movement metrics within analytical tools for resource selection modelling can provide information on the animal's choices of location in relation to spatial covariates: for example, step selection functions (SSFs) can offer insights into the selection or avoidance of different habitat types (Fortin et al. 2005; Thurfjell et al. 2014).

Because spatial heterogeneity in risk creates landscapes in which locations differ in their potential fitness costs, consistent individual differences in the selection of risky areas estimated through SSFs may thus provide a proxy for inter-individual differences in risk-taking (Brogi et al. 2022). Exploration can be quantified by

measuring the speed of exploration of a novel environment, or alternatively the proportion of a new environment explored (Minderman et al. 2009); similarly, SSFs can be used to estimate exploration by quantifying the tendency to select novel areas. Activity is defined as the “general level of activity of an individual” (Réale et al. 2007) and can be calculated using quantitative indicators of distance travelled and time spent moving (McMahon et al. 2023; Santicchia et al. 2021; Thomson et al. 2020).

These traits have been shown to be repeatable, e.g. activity level in barnacle geese, *Branta leucopsis* (Kurvers et al. 2009), and exploration in starlings, *Sturnus vulgaris* (Minderman et al. 2009). There is evidence from numerous species that some individuals are always more exploratory than others (Dingemanse et al. 2004; Schuett et al. 2011, Brogi et al. 2022) and that more explorative individuals are more risk-prone and have higher levels of aggression than less exploratory ones (Groothuis et al. 2005).

Movement metrics require animal spatial positions that are sufficiently accurate both qualitatively and quantitatively. As they can provide high temporal-resolution location data, biologging and GPS telemetry allow for a detailed quantification of the spatial and movement behaviours of free-ranging animals (Cagnacci et al. 2010; Boon et al. 2008; Hertel et al. 2020).

Research on piscivorous pike, *Esox lucius*, conducted with radio telemetry methods showed highly conserved individual movement strategies, recognizing three behavioural types based on activity patterns and habitat use. Two of the three behavioural types in pike showed strong habitat fidelity to either reedbed or submerged macrophyte habitats, while the third type was an opportunistic mover, using all habitats including the pelagic zone (Kobler et al. 2009).

Another example is the study on brown bears (*Ursus arctos*) by Hertel et al. 2019. A multivariate mixed model revealed significant positive correlations between daily travelled distance, daily displacement and diurnality, suggesting the existence of an activity–exploration and potentially partial boldness syndrome in a

bear population (Hertel et al. 2019). However, the limitation of these movement metrics is that the expression of a behaviour (e.g., step length) may be repeatable, but it does not necessarily represent a behavioural choice; in contrast, selection patterns estimated through SSFs are more likely to capture such behavioural propensities.

1.5 Study aims, Hypothesis, and Predictions

In recent decades, research on “animal personality” has greatly expanded; however, there are still few studies conducted on large wild mammals because they are more difficult to study experimentally. The available works show that also in these taxa there are repeatable personality traits, linked to space use, activity, social structure, and risk management. This study proposes itself as one of the first in which the risk-taking – activity – exploration axis is investigated through movement ecology models in order to formally test POLS theory.

The mountain-dwelling Alpine chamois (*Rupicapra rupicapra*) constitutes an ideal model for testing POLS theory in a wild population. Its strongly polygynous mating system generates potentially pronounced variation in male reproductive strategies across individuals (Apollonio et al. 2020), offering the possibility to investigate not only consistent inter-individual behavioural differences and their correlation in syndromes, but also their outcomes in terms of reproductive success. Moreover, like in other ungulate species, sex-specific life-history, such as forage-safety trade-offs, gives rise to particularly pronounced sexual behavioural dimorphism (Edelhoff et al. 2023). To enhance mating success, males typically prioritize growth and reserve accumulation, whereas females prioritize survival and offspring care (Main 2008; Grignolio et al. 2007; Ciuti et al. 2008). Investigating also these sex-specific differences is therefore a key aspect to understanding behavioural strategies in this species.

In line with behavioural syndrome theory (Wilson et al. 2009; Garamszegi et al. 2009; Hughes et al. 2025), I tested the hypothesis of the occurrence of a risk-taking - activity - exploration syndrome in the Alpine chamois (H1a) and of its

reflection in systematic differences between the sexes, with males showing higher levels of all three behaviours than females (H1b).

Then, in line with the Pace-of-Life Syndrome (POLS) theory, I hypothesized that “fast”, highly risk-prone, active and explorative male chamois adopt a more capital breeding strategy (H2a), exhibit higher short-term reproductive effort and achieve greater short-term reproductive success than “slow”, risk-avoiding, less active, less explorative individuals (H2b).

In this study I analysed a GPS-tracking dataset collected in 2023-2025 from 27 wild Alpine chamois (12 females and 15 males) on the Monte Grappa Massif (NE Italy) to extract individual patterns of: selection for risky areas (risk-taking), site fidelity (exploration), and activity. Risky areas were defined using a risk map, constructed from the spatial distribution of wolf predation events, and site fidelity was quantified as the temporal rate of return to previously visited areas. Behavioural observations recorded during two consecutive rutting seasons (2024 and 2025) provided independent estimations for the individual males' reproductive effort and reproductive success.

The effort was assessed using proxies such as frequencies of vigilance events, time spent feeding, resting, interacting with other males, and engaging in agonistic behaviours like scent marking and body-head shake. The average number of females a male occurred with was used as a proxy for reproductive success.

Based on the hypothesis presented above, I formulated the following predictions:

P1a) chamois will exhibit time consistent inter-individual differences in their tendency to select for risky areas (risk-taking), their tendency to select for novel areas (exploration) and their activity levels, and these behaviours will covary positively at the individual level, in both males and females

P1b) Sexes will differ in the behavioural gradient, with females showing lower levels of risk-taking, activity, and exploration than males

P2a) in males, “fast” risk-prone, more explorative and more active individuals will exhibit a lower tendency to forage during the rutting season, revealing a more pronounced capital breeding strategy compared to their “slow” counterparts (risk-avoider, less explorative, less active, and more intense forager during the rut)

P2b) fast males will exhibit a more intense reproductive effort during the rutting seasons, i.e., fewer vigilance events, less time spent resting, more time in interaction with other males and more frequent agonistic behaviours such as scent marking and body-head shake. Moreover, they will achieve more reproductive opportunities, occurring with a higher number of adult females.

2. MATERIALS AND METHODS

2.1 Study Area

The study was conducted in the Monte Grappa, an extensive mountain complex located in the Venetian Prealps area, Northeastern Italy. Monte Grappa has a wide surface, covering approximately 400 km² and lying at the intersection of the provinces of Vicenza, Treviso, and Belluno. The vertical relief is about 1,500 m, from the valleys opening onto the plain up to the highest peak, Cima Grappa (1,775 m a.s.l.). The area is characterized by a peculiar topography, with steep cliffs bordering the lower sections of the massif and smoother slopes and meadow habitats occurring above approximately 1,000 m a.s.l.

It rises directly from the Venetian plain, leaving it exposed to adverse weather conditions and frequent mist ascending from the plain. The climate is suboceanic pre-Alpine, comparable to that of the central-northern Apennines: winters are

moderately cold and snowy, with temperatures frequently dropping below 0 °C at higher elevations, while summers are mild and rarely exceed 25–28 °C (Baggio 1985; Bon 2017).

The forest cover is dominated by silver fir (*Abies alba*), Norway spruce (*Picea abies*), and beech (*Fagus sylvatica*); the high presence of conifers largely results from anthropogenic reforestation (Busnardo et al. s.d.).

Until the early 2000s, the alpine chamois was restricted to the lower-altitude, steep western slopes of the massif, in the valley of Valsugana (Dal Compare 2008). Restocking measures in the 2000s (see Dal Compare 2008), successfully led to the repopulation of the massif, which now hosts a permanent and steady chamois population, with an important concentration around the summit in the area known as Cima Grappa.

Other ruminant species present in the massif include roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and, to a lesser extent, European mouflon *Ovis aries musimon*. The population densities of these species, estimated from hunting bags, are 3.34, 1.43, and 0.84 individuals/km², respectively, while the average density for the chamois is 1.68 individuals/km² (Cavazza et al. 2026). The wolf *Canis lupus* is currently present in the massif and serves as the only predator to chamois besides humans.

Wildlife monitoring and hunting plans are managed annually by the provinces of Vicenza, Treviso, and Belluno. Monte Grappa is also a major tourist destination, known for cycling routes, hiking trails, and paragliding launch sites.

2.2 Study Species

THE NORTHERN CHAMOIS

Class: Mammalia

Order: Artiodactyla

Family: Bovidae

Subfamily: Caprinae

Species: *Rupicapra rupicapra*



Figure 1. Adult female of Alpine chamois from the population of monte Grappa

Chamois are mountain caprines found in most major mountain ranges of Western and Eastern Europe, extending as far as the Caucasus range in the Near East.

The Alpine chamois (*Rupicapra rupicapra rupicapra*) exhibits strongly seasonal sexual dimorphism, with differences in body mass increasing throughout the summer and becoming particularly pronounced during the rut. Adult males (*Figure 2*) typically weigh between 30 and 45 kg and measure approximately 76-86 cm in height and 120-135 in length. Females (*Figure 1*) are slightly smaller with a weight from 25 to 35 kg, a height of 66-76 cm and a length of 110-130 cm (Corlatti et al. 2022).

The reproduction period occurs from early November to early December, peaking between November 20th and 30th (Mustoni et al. 2002). During this time males become more aggressive; some adopt territorial strategies, spending energy in active defence of small area (200-500 m in diameter) from rival males and in ritualized courtship to maintain groups of females in this zone. This suggests they defend the territory rather than the group of females directly. The energy expenditure of males during rut can cause a reduction of more than 15% of their body mass, for this reason chamois is considered a capital breeder species (Apollonio et al. 2020). The polygynous mating system of this species is characterized by a strong predominance of male–male (intrasexual) selection over intersexual selection. Female choice, if present, indeed represents a very small component of male reproductive success compared to the level of territoriality and

dominance in the male hierarchy (Apollonio et al. 2020; Corlatti et al. 2012, 2015). However, in contrast with patterns described in other Alpine populations (Corlatti et al. 2012), male chamois of the population monitored in this study showed no evidence of alternative mating tactics in terms of territoriality (Brogi et al. under review).

The Alpine chamois is a mostly diurnal ruminant species that occupies a broad elevational gradient, ranging from about 600–800 m a.s.l. to the nival zone, and is characterized by pronounced seasonal movements along altitude. In the summer period, individuals primarily inhabit open habitats at high elevations, including alpine grasslands, rocky outcrops, scree fields, and ledges, while also making use of subalpine coniferous forests during daily transitions between feeding and resting areas. Forest habitats are further exploited as shelter from anthropogenic disturbance, particularly during periods of intense tourist presence (Bon 2017). During winter, chamois descend to lower altitudes and tend to favour south-facing slopes, where steeper terrain, reduced snow cover, and lower levels of disturbance facilitate access to essential food resources. This season corresponds to the highest mortality rates for the species (Bon 2017). A key ecological requirement for the species is the availability of steep rocky terrain or cliffs, which function as critical escape habitats (Apollonio et al. 1984; Elsner-Schack 1985).

The diet of the Alpine chamois is mainly based on graminoids (Redjadj et al. 2014). As an intermediate feeder, its diet composition varies seasonally: in summer it includes both forbs and graminoids, whereas in winter it shifts towards a higher consumption of woody vegetation such as shrubs and coniferous material (Andreoli et al. 2016)



Figure 2. A male of Alpine chamois at rest, fitted with ear tags to allow individual identification from a distance.

2.3 Data collection

2.3.1 Captures and GPS-tracking

Capture and collaring activities were carried out within a broader research project of the University of Sassari, in collaboration with the provincial police forces of Treviso, Vicenza, and Belluno, following the protocols outlined in Brogi et al. 2026. The procedures were performed by specialized personnel and a veterinarian during a total of five capture sessions between June 2023 and March 2024. The capture areas were located within the territory of the Province of Treviso, specifically in the areas of Cima Grappa, Rifugio Ardosetta, and Pian dela Bala.

During the first three capture sessions performed in 2023, 11 males were captured using chemical immobilization via darting guns. To protect young chamois, females were not targeted during this period of parturition and nursing. From September 2023 onwards, darting guns were then replaced by a drive-netting method, which allowed for the simultaneous capture of multiple individuals.

Under the supervision of a veterinarian, each captured individual was measured, weighed, and aged by counting horn growth rings. Tissue samples were collected, and everyone was marked with a unique combination of coloured ear tags to allow field identification (*Figure 3*) (M or F to indicate sex, followed by a serial number, e.g. the third male was named M03).

GPS collars, supplied by VECTRONIC Aerospace (Berlin, Germany), were fitted to a total of 27 adults (aged ≥ 2 years), comprising 15 males and 12 females by session: June 2023: 7 males; July 2023: 3 males; September 2023: 3 females; December 2023: 1 male; March 2024: 4 males, 9 females (*Figure 4*).

The collar data collection settings were configured to achieve the best balance between data resolution and battery life. The sampling frequency of GPS locations was one fix per hour (± 10 min tolerance). In addition, the collars incorporated tri-axial accelerometers that measured acceleration at 8 Hz, with averaged values recorded at 5-minute intervals.

Each collared chamois can be monitored through an interactive map provided on the VECTRONIC Aerospace website, where location data are updated every two hours. More detailed information, including higher-resolution GPS fixes (one per hour) and activity records collected via the collar's accelerometer, can only be retrieved in the field by connecting to the device through a VHF radio.

The collar sampling period for this study began with the first males captured in June 2023 and ended in late September 2025, when only a few collared males remained. Because individuals were not captured simultaneously, sampling effort varied among individuals. This variation was accounted for by incorporating sampling effort as a weighting factor in the subsequent statistical analyses.



Figure 3. Collared and marked adult male (M15), from the studied population of Alpine chamois



Figure 4. Collared and marked adult female (F04), from the studied population of Alpine chamois

2.3.2 Behavioural data from observation in the field

Behavioural observations were conducted through field video recordings for two consecutive reproductive seasons: years 2024 and 2025. The specific time frame was from November 9th to December 18th, 2024, and from November 4th to December 21st, 2025.

Videos were 30 minutes long; only a subset had shorter durations, and only those above 5 minutes were kept. Recordings focused on individuals in open areas to allow clear visualization of animal behaviour. Up to two videos were taken for each animal and day, resulting in a maximum of 60 minutes of video footage per animal per day. By the end of the period, the aim was to have each animal filmed at least three times, the optimal being five. Observations of the same animal were spaced for at least some days to prevent autocorrelation: five days in 2024 and reduced to three days in 2025. Each recording was matched with the corresponding location and timestamp of the video. When possible, cameras and observers were positioned at a sufficient distance (50-200 m) to minimize disturbance to the animals.

Video analysis was performed using BORIS (Behavioural Observation Research Interactive Software) (Friard et al. 2016). BORIS is a free, open-source program for user-defined behavioural coding of previously recorded videos or live observations. The ethogram applied in the present study (Corlatti et al. 2013; Krämer 1969) is reported in the table below (*Table 1*). Video recordings were coded independently by four trained observers. Each coder was first trained using a set of videos and then inter-observer reliability was assessed on 30% of the total video records, separately for each year. Coding consistency was quantified using intraclass correlation coefficients (ICCs), which were calculated at the beginning and again at the end of the coding process. Only behavioural categories with high reliability ($ICC \geq 0.6$) were retained for subsequent analyses. It was not possible to calculate the intraclass correlation coefficients (ICCs) across years because the records were coded by a different pair of coders in each year.

Each observation corresponds to the sum of all behaviours observed within a single video recording. Behaviours were divided into two main categories: **STATE behaviours**, for which the time spent performing a specific behaviour was recorded, and **POINT behaviours**, for which only the number of occurrences within each video recording was considered.

Behaviour	Description	ICC	
		2024	2025
Feeding	The subject is grazing, with its head mostly down, despite eating periods may be interspersed by head up events. (State)	0.984	0.955
Rest	The subject is lying on its chest and abdomen, or on its side. Legs may be underneath the body or stretched out. (State)	0.999	0.966
Marking	Head or horns are rubbed on a plant or other supports. (State)	0.802	0.980
Number females	The (minimum ascertained) number of adult females within 50 m from the focal subject. (State)	0.823	0.939
Male – male interaction	It should last as long as two males are in sight: it may be just one per observation. Coded also when two males are apparently ignoring each other. (State)	0.682	0.845
Head - up	When eating, the subject raises the head above the horizontal line of the back for less than 5 seconds, to distinguish it from Stand. It should not be coded for resting subjects. (Point)	0.667	0.963
Body – head shake	A standing male shakes its head and body, often while urinating, to spread scent. To be coded also in absence of other males. (Point)	0.763	0.947

Table 1. Ethogram with description and ICC (= Intraclass Correlation Coefficient) of relevant behaviours.

Behaviours such as feeding, resting, marking, interactions with other males, head-up, and body-head shake were selected as representative of reproductive effort. Differences in time spent feeding reflect alternative strategies of energy allocation, as predicted by the capital–income breeding system (Stephens et al. 2009). The frequency of head-up behaviour and the time spent resting are indicative of individual vigilance level. Interactions with other males, marking and frequencies in body-head shake provide a measure of reproductive effort, as these behaviours are directly related to reproductive function (Corlatti et al. 2013).

The reproductive success was estimated considering the presence of females in proximity to the male in terms of quantity and time (L'Italien et al. 2012). An index of weighted mean was then utilized to associate the number of females to the time in which they remained within a 50 m distance from the male individual. The index was calculated for each video, using the following formula:

$$\frac{\sum_i^k Fi \cdot Si}{\sum_i^k Si}$$

With Fi = number of females per observation

Si = time duration of each observation

2.4 Statistical analysis

2.4.1 Movement traits calculation

Movement behaviours were computed through proxies obtained from biologging data collected by collars. The movement traits investigated were activity, risk-taking and exploration; GPS locations were used in the analysis of risk-taking and exploratory behaviour, while the individual level of activity was calculated through data from triaxial accelerometers.

Because the aim of the study was to relate individual variation in spatial behaviour to male reproductive behaviour, the three GPS-derived traits were analysed through data collected during spring and summer (April–September). In Alpine chamois, males acquire the energetic resources required for reproductive effort during this period (Stephens et al. 2009), making it the most appropriate season in which to quantify risk-taking, activity, and exploration.

All models were fitted in a Bayesian framework with the *brms* package (Bürkner 2017, 2018), which interfaces R to the Stan platform (Carpenter et al. 2017) through the *cmdstanr* backend. In every model, repeatable among-individual differences were captured by individual-level random effects, following the mixed-model approach to quantifying individual variation in behaviour (Dochtermann et al. 2013). Models were sampled with Hamiltonian Monte Carlo (the No-U-Turn sampler); weakly-informative priors were used throughout, and convergence was assessed from the rank-normalised R-hat statistic (all R-hat < 1.05) and from divergent-transition diagnostics (Vehtari et al. 2021).

Activity

An hourly activity proportion was computed as the share of active records within each GPS hour; to distinguish between active and inactive states from raw accelerometer data, threshold values were established following the procedure proposed by Brivio et al. (2021). This proportion, bounded in $[0, 1]$ with exact 0s and 1s, was modelled with a zero-one-inflated beta distribution (Ospina et al. 2012) on a logit link, which jointly models a beta-distributed proportion and the

probabilities of the boundary values 0 and 1. Predictable temporal structure was absorbed with penalized regression splines, i.e. a generalized additive model (Wood 2017): a cyclic cubic spline of hour-of-day captured the circadian rhythm and a cubic-regression spline of day-of-year the seasonal cycle. A subject-level random intercept quantified repeatable among-individual differences in overall activity, the quantity of interest (*Figure 5*). The model structure was:

```
activity_proportion ~ s(jdate, bs = "cr") + s(hour, bs = "cc") + (1 | Subject)
# family: zero_one_inflated_beta() (logit link)
```

i.e. a cubic-regression spline of day-of-year (*jdate*), a cyclic cubic spline of hour-of-day (*hour*, so that 23:00 joins 00:00 smoothly), and a subject-level random intercept.

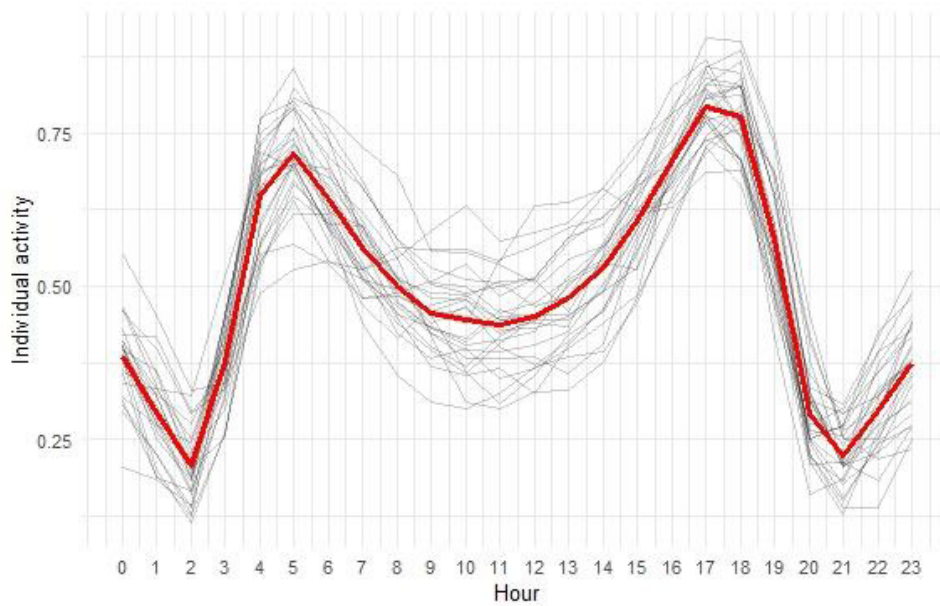


Figure 5. Males and females' daily activity

The graph depicts mean daily activity patterns in 15 males and 12 females from the studied population of Alpine chamois, based on data from April 1 to September 30 for both 2023 and 2024. Individual activity on the y-axis is the proportion between 0 and 1 of the mean individual activity level per hour. The x-axis represents the daytime in 24 hours scale. The grey lines describe each individual mean variation of activity during the day, while the red line shows the overall mean variation of all individuals.

Step-selection functions: exploration and risk-taking

GPS tracks were processed with the *amt* package (Signer et al. 2019): per individual, tracks were resampled to a regular one-hour step duration (ten-minute tolerance) and split into bursts of consecutive regular fixes, from which observed steps were derived. For each observed step, 20 alternative (“available”) steps were generated by sampling step lengths from a gamma distribution and turning angles from a von Mises distribution, both fitted to each individual’s own observed steps (Signer et al. 2019).

Exploration and risk-taking were estimated within a single model: the random steps were simulated once and both covariates were read at the same step endpoint, so that the two selection coefficients share one posterior and their among-individual correlation is identified within the model rather than reconstructed from separate fits.

Matched used/available step sets were analysed as a conditional logistic regression implemented as an equivalent Poisson model with stratum-specific (per step) intercepts, following Muff et al. (2020): the standard deviation of the stratum intercepts was fixed at a large value (1000) and the global intercept omitted, while individual variation in selection was modelled as animal-level random slopes on both covariates.

Selection coefficients are interpreted on the relative-selection-strength (RSS) scale, i.e. the exponentiated change in the relative probability of use per one-standard-deviation increase in the covariate (Fieberg et al. 2021).

The two covariates were derived as follows. For exploration, a hexagonal grid (18 m side length, approximately 840 m² in area and 31 m between opposite edges) was overlaid on the study area and the end point of every step (used and available) was assigned to a cell; we then computed the time elapsed since that cell had last been visited by the same individual. This interval spans about five orders of magnitude, from a few minutes to roughly two years, and therefore entered the

model on the log scale after standardization; a positive coefficient indicates selection for long-unvisited cells, i.e. an exploratory, novelty-seeking tendency.

For risk-taking, the end point of every step was annotated with a spatially explicit wolf predation-risk surface (30 m resolution). The risk map used in this study was developed in previous research using a habitat selection model fitted to telemetry data from four wolves belonging to packs in the study area between 2020 and 2024 (Brogi et al. under review) (*Figure 6*).

The model allowed the probabilistic description of wolf selection for environmental variables at chamois predation sites. These were found to be consistent with the macro-morphological characteristics of the terrain and in line with the literature on this predator. For these reasons, although the risk distribution raster file does not perfectly overlap temporally with the data used in the present study, it is still considered valid for inferring the investigated behaviour.

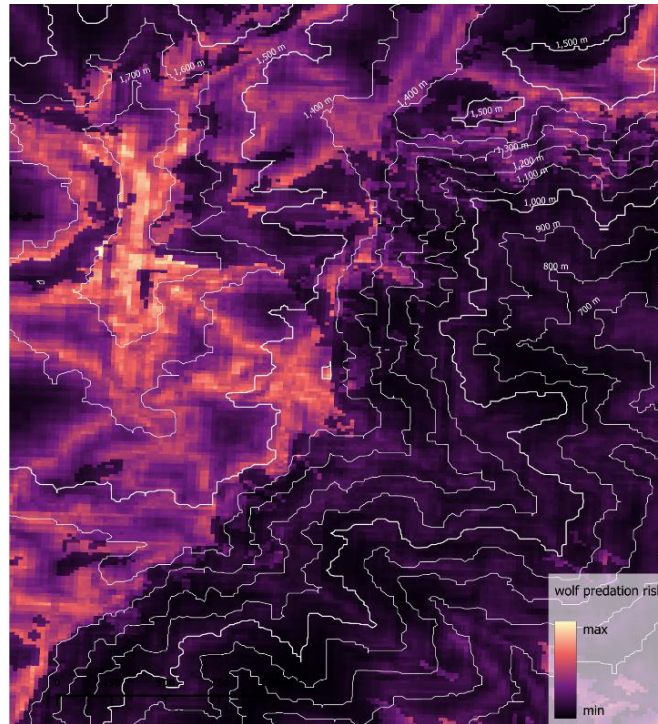


Figure 6. Predicted landscape of wolf predation risk

Image extracted from the raster file of the risk map for Alpine chamois across the Monte Grappa Massif, based on a spatial model fitted to 238 confirmed predation events by four GPS-collared wolves between 2020 and 2024.

The standardized predation-risk value was the second selection covariate, and a negative coefficient indicates avoidance for higher-risk locations, a positive one a selection for it. The three movement terms of an integrated step-selection analysis (step length, its logarithm and the cosine of the turning angle) were also included, in order to correct the movement kernel used to generate the available steps (Avgar et al. 2016). The model structure was (family: poisson, the conditional-logistic-Poisson equivalence of Muff et al. 2020):

```
case ~ -1 + z.wolf_risk:sex + z.log_time_diff:sex +
      log_sl + sl + cos_ta +
      (1 | stratum) +
      (0 + z.wolf_risk + z.log_time_diff | animal_id)
```

where case codes used (1) versus available (0) steps, (1 | stratum) are the per-step intercepts, whose standard deviation is fixed at 1000 and whose identifier is unique to each animal-by-step combination, and (0 + z.wolf_risk + z.log_time_diff | animal_id) are the individual random slopes on the two covariates, with no individual intercept (absorbed by the stratum term) and with their among-individual correlation estimated. Priors were a constant of 1000 on the standard deviation of the stratum intercepts, Normal (0, 5) on the selection and movement coefficients, Normal (0, 3) on the among-individual standard deviations of the slopes. The model was fitted with four chains of 2000 iterations each (1000 of warm-up).

2.4.2 Among-individual (co)variance of rut behaviours

The seven behaviours resulting from ethogram analysis were analysed jointly in a single multivariate (multi-response) model so that individual differences could be estimated on a common latent scale. The cumulative durations of feeding, resting and male–male interaction, and the number of controlled females, were modelled with hurdle-gamma distributions; scent-marking with a hurdle-lognormal distribution; and the counts of head-up vigilance and of body-head shake with zero-inflated Poisson distributions.

Each response had a fixed effect of coding duration to control for unequal observation effort, and a subject-level random intercept. Adjusted repeatability for each behavioural index was calculated as the proportion of variance explained by the subject-level random effect relative to the sum of the subject-level random-effect and residual variances, based on this model. Default weakly-informative *brms* priors were used, including an LKJ=1 prior on the random-effect correlation matrix (Lewandowski et al. 2009).

To assess the potential effect of age on the proxy of reproductive success (number of females), a Spearman rank correlation was performed between individual male age and the corresponding mean number of females observed with each male for each study year.

2.4.3 Individual estimates and back-transformation

From each model we extracted the full posterior distribution of the individual-level effects: the subject random intercepts for activity and for each rut behaviour, and the animal-level random selection slopes for exploration and risk-taking.

To express these on interpretable scales, each individual deviation was combined with the relevant population-level term and back-transformed through the model's inverse link: for activity, added to the population intercept and inverse-logit transformed (mean activity proportion per individual); for the two SSFs, added to the sex-specific fixed slope and exponentiated (individual relative-selection-strength coefficient); and for the rut behaviours, added to the behaviour intercept and the coding-duration effect evaluated at the mean focal-sample length, then exponentiated (expected behaviour during an average-length observation).

2.4.4 Among-individual axis and behavioural alignment

To test for an integrated among-individual axis of the kind predicted by the behavioural-syndrome and pace-of-life frameworks (Sih et al. 2004; Réale et al. 2007, 2010; Dingemanse et al. 2010; Spiegel et al. 2017), we combined the three GPS-derived traits: activity, exploration and risk-taking, all oriented so that higher values denote a more active, more exploratory and more risk-prone phenotype, and submitted them to a principal component analysis on standardized traits (Budaev 2010).

The PCA was performed on the full posterior rather than on point estimates; the analysis was re-run on each set of joint posterior draws, yielding a posterior distribution of the variance explained by each component and a posterior distribution of the loadings.

Within each draw the sign of the first axis (PC1) was aligned to a common reference loading vector (from a single PCA of the posterior-mean traits) so that scores and loadings were comparable across draws, and each individual was assigned its per-draw PC1 score. The whole procedure was carried out separately for males ($n = 15$) and for females ($n = 12$), each sex being standardized within-sex population, so that the two sexes are described by independent axes rather than by a single axis constrained to be common to both.

Finally, restricting the analysis to the males for which rut behaviour was available ($n = 14$), we asked whether an individual's position on this axis was associated with its single rut behaviours, including the average number of females as a proxy of reproductive success.

Each observed posterior was compared with a null obtained by permuting individuals within each draw, and the observed and null distributions were contrasted with a two-sample Kolmogorov–Smirnov (KS) test. The p-value of this test has no meaning since it is performed on the full posteriors and thus with a

huge sample size and thus a minimal difference in the means would result in a very low p-value.

For this reason, we considered the distribution significantly different only if the maximum vertical distance between distributions (D) exceeded 0.2 (Marsaglia et al. 2003). Because the correlations were computed on the full joint posterior rather than on fixed point estimates, this propagates the uncertainty of the individual estimates into the correlations and avoids the anticonservatism of two-step analyses of best linear unbiased predictors (Houslay et al. 2017; Dochtermann et al. 2013). All analyses were carried out in R (R Core Team 2024) with the *brms*, *amt*, *posterior*, *mgcv* and *tidyverse* packages.

3. RESULTS

3.1 Among-individual variation in each trait

We report the mean results of the posterior and the 95% credible interval between brackets.

Activity. Overall activity was centred on a population mean proportion of 0.48 [0.48, 0.49].

Exploration. At the population level, chamois selected against long-unvisited cells — that is, they showed site fidelity rather than novelty-seeking: the standardized selection slope on time-since-last-visit was -0.56 [$-0.58, -0.54$] in females and -0.61 [$-0.63, -0.59$] in males (RSS of 0.57 and 0.54 per one-SD increase).

Risk-taking. Population-level selection on wolf predation risk was essentially neutral: -0.02 [$-0.09, 0.06$] in females and $+0.06$ [$0.03, 0.09$] in males (RSS = 1.06), i.e. at most a weak tendency for males to select riskier locations (*Figure 7*).

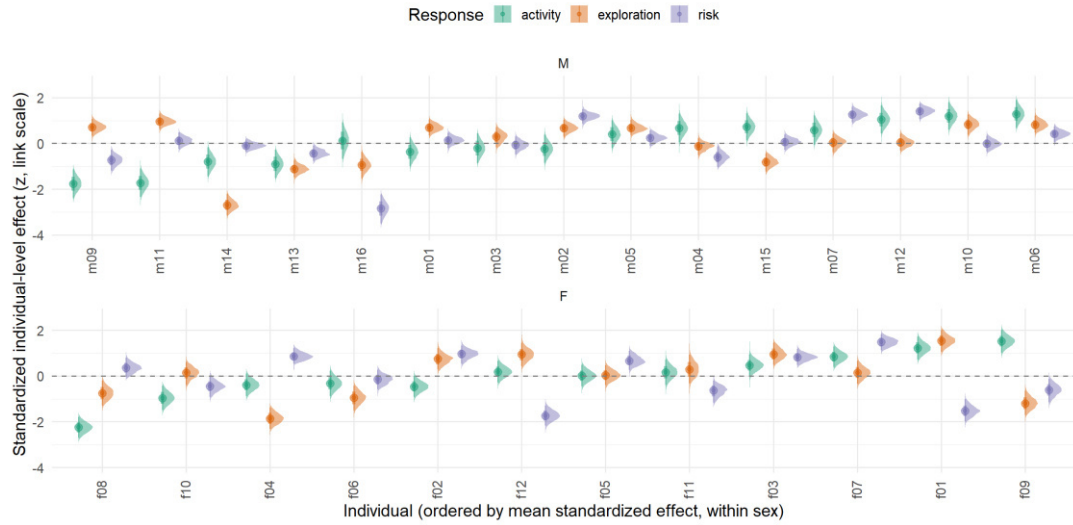


Figure 7: Individual levels model estimates.

Risk and exploration are extracted from step selection function models' individual random slopes, their unit of measurement is thus relative-selection-strength, i.e. the individual estimate of the angular coefficient. Activity, the individual level intercept, is in standard deviation units from the fixed effect intercept. Since the difference in scales, all the draws have been scaled, to obtain comparable magnitudes for plotting. The full posterior density of the estimates is displayed, with the slab shown as thin and thick lines indicating the 89% and 50% credible intervals, respectively, and the point indicating the posterior mean.

Rut behaviour. Among-individual variation was clearest for the two point behaviours — body-head shake (SD = 0.88 [0.46, 1.64]) and head-up vigilance (0.69 [0.41, 1.19]), whose credible intervals were well above zero — and weaker and more uncertain for the duration behaviours (scent-marking 0.45 [0.04, 1.03], eating 0.30 [0.04, 0.66], n females 0.25 [0.02, 0.71], male–male interaction 0.17 [0.01, 0.44], resting 0.12 [0.01, 0.41]), whose lower interval bounds approached zero. Among-individual correlations among rut behaviours were weak and every credible interval overlapped zero (largest $|r| \approx 0.32$ for eating vs body-head shake, $[-0.79, 0.35]$), giving no evidence for a within-ethogram behavioural syndrome (Figure 8).

The proportion of variance explained by the individual-level random effect in the model, after controlling for fixed effect of coding duration, provided a measure of adjusted repeatability for each behavioural index (Figure 9). Body-head shake and head up were the only behaviours with a mean adjusted repeatability greater than 30%, whereas all the others showed percentage distributions with mean values below 20%.

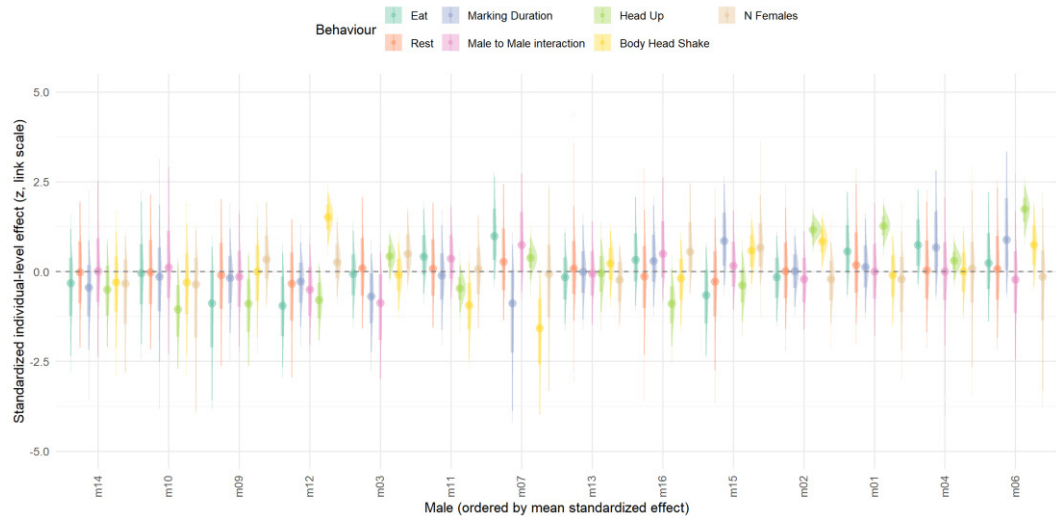


Figure 8. Individual levels of rut behaviours model

Among-individual variance–covariance in each rut behaviour is extracted from multivariate (multi-response) models’ random intercepts. For further details on the selected behaviours, see Section 2.3.2 of the main text. Since the differences in scales between point and duration behaviours, draws have been scaled to obtain comparable magnitudes for plotting, allowing individual differences to be estimated on a common latent scale. The posterior estimates are shown as slabs, with thin and thick lines indicating the 89% and 50% credible intervals, respectively, and the point indicating the posterior mean. The x axis is ordered based on the individual mean standardized effect.

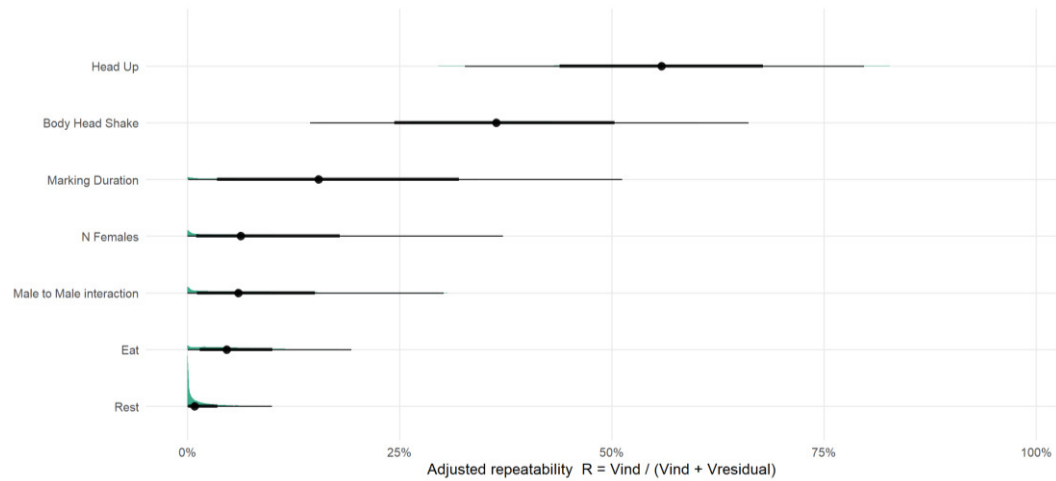


Figure 9. Adjusted repeatability of selected rut behaviours in male Alpine chamois

Adjusted repeatability was estimated from field observations collected from 14 male Alpine chamois during the reproductive periods (November–December) of 2024 and 2025. For each behaviour, adjusted repeatability was calculated as the ratio of the individual-level random-effect variance to the sum of the individual-level random-effect and residual variances, and expressed as a percentage. These values were extracted from the model including coding duration as a fixed effect. For further details on the selected behaviours, see Section 2.3.2 of the main text. The posterior estimates are shown as slabs, with thin and thick lines indicating the 89% and 50% credible intervals, respectively, and the point indicating the posterior mean.

The indicator number females was used as a proxy of reproductive success for single mating season; it is plotted in the histogram below (*Figure 10*). For two subjects, M09 and M10, it was possible to estimate it in only one season, and M05 in none of them, this due to the lack of observation collected in the field.

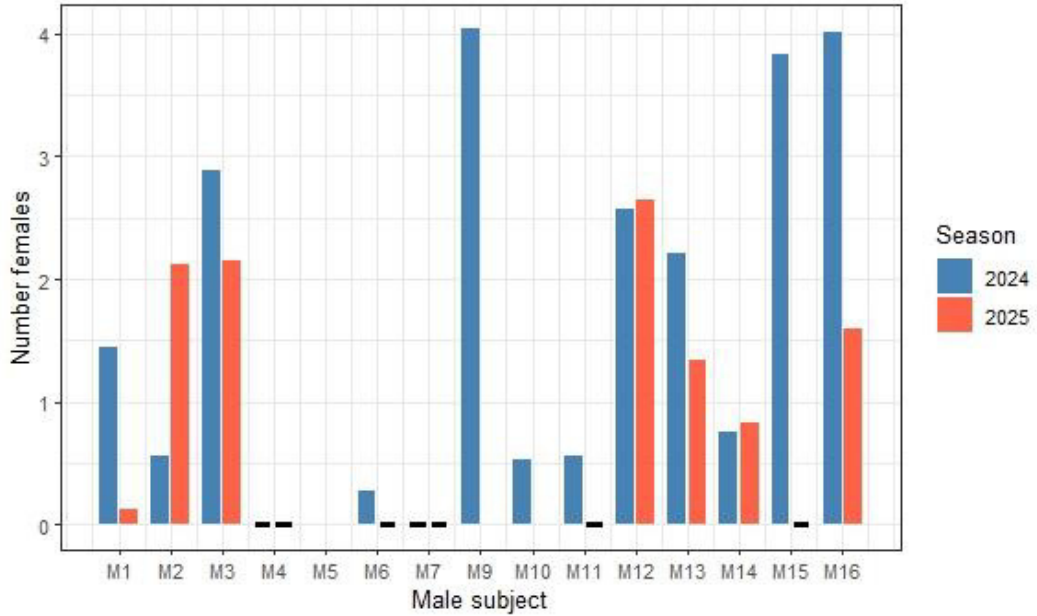


Figure 10. Mean number of females observed per male in each reproductive season

The histogram represents the mean number of females observed per each male Alpine chamois during the reproductive seasons of 2024 and 2025. Black lines indicate that 0 females were observed with that male in that year. The absence of a symbol indicates that no observation was collected for that male in that year.

3.2 A personality / pace-of-life axis (full-posterior PCA)

Computing the PCA over the full posterior separately within each sex, in males the first axis explained 48.0% [41.7, 55.0] of the variance, ahead of PC2 (30.9% [25.5, 35.9]) and PC3 (21.2% [16.7, 26.0]); in females it explained 50.8% [43.2, 58.1], ahead of PC2 (27.8% [23.1, 32.9]) and PC3 (21.4% [16.8, 26.3]) (*Figure 11*). In both sexes the credible interval for PC1 thus excluded the one-third expected under no structure, but PC1 nonetheless accounted for about half of the total variance, indicating that the three traits are far from collinear (*Figure 13*).

In males all three traits loaded positively on PC1 with high posterior certainty; risk 0.67 [0.57, 0.74], exploration 0.58 [0.39, 0.71] and activity 0.49 [0.03, 0.62], each with $P(\text{loading} > 0) \geq 0.98$ (the activity loading the smallest and most variable). In females, exploration 0.61 [0.49, 0.70] and activity 0.56 [0.34, 0.66] also loaded positively, whereas risk loaded negatively, $-0.58 [-0.68, -0.41]$ with $P(\text{loading} > 0) = 0.00$ (*Figure 12*).

In males PC1 therefore describes a coherent, consistently signed gradient along which more active individuals also tend to select less-recently-visited and higher-risk locations, consistent with an among-individual pace-of-life / boldness axis; in females the same axis combines activity and exploration with avoidance, rather than selection, of risky locations (*Figure 14*).

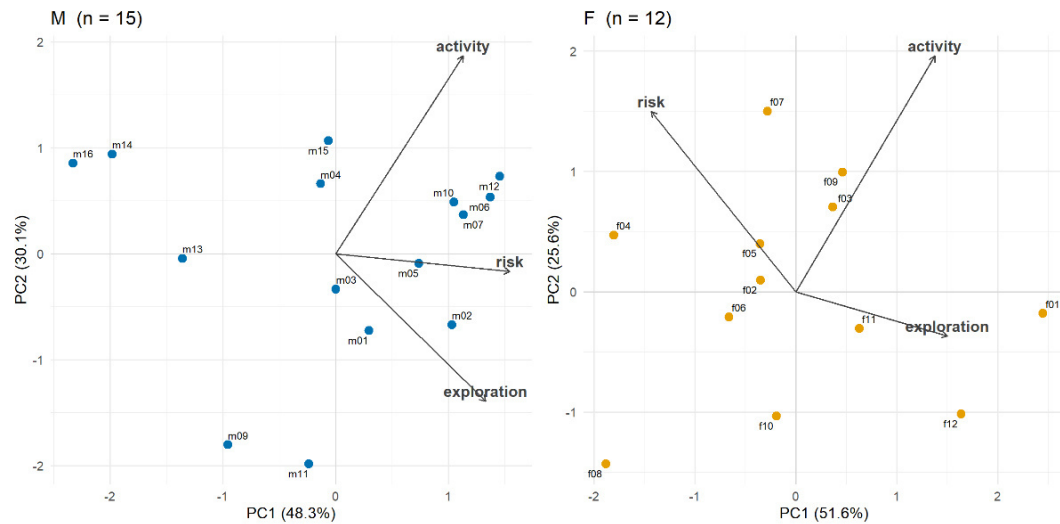


Figure 11. PCA biplot of individual scores

Individuals are displayed according to their coordinates on the PC1 and PC2, calculated from the posterior mean values. Points represent the positions of the studied Alpine chamois along the PC1 and PC2 axes, while arrows indicate the direction of the behavioural loadings on the two axes.

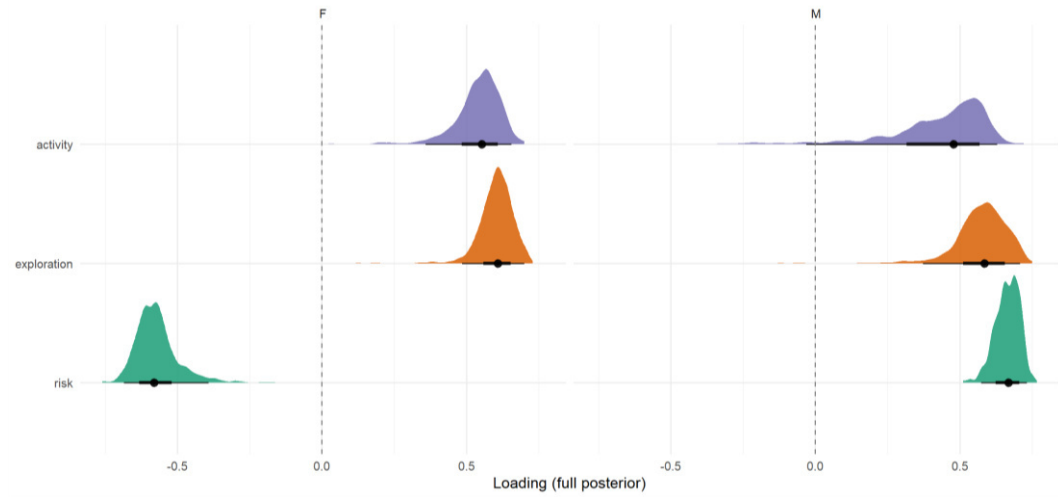


Figure 12. Full posterior PCA trait loadings by sex

The two panels show the full posterior distribution of the trait loadings on the PC1 axis by sex, calculated from 15 males and 12 females of Alpine chamois. Female loadings are shown on the left, whereas male loadings are shown on the right. Slabs indicate the 89% and 50% credible intervals as thin and thick lines, respectively, with the point indicating the posterior mean.

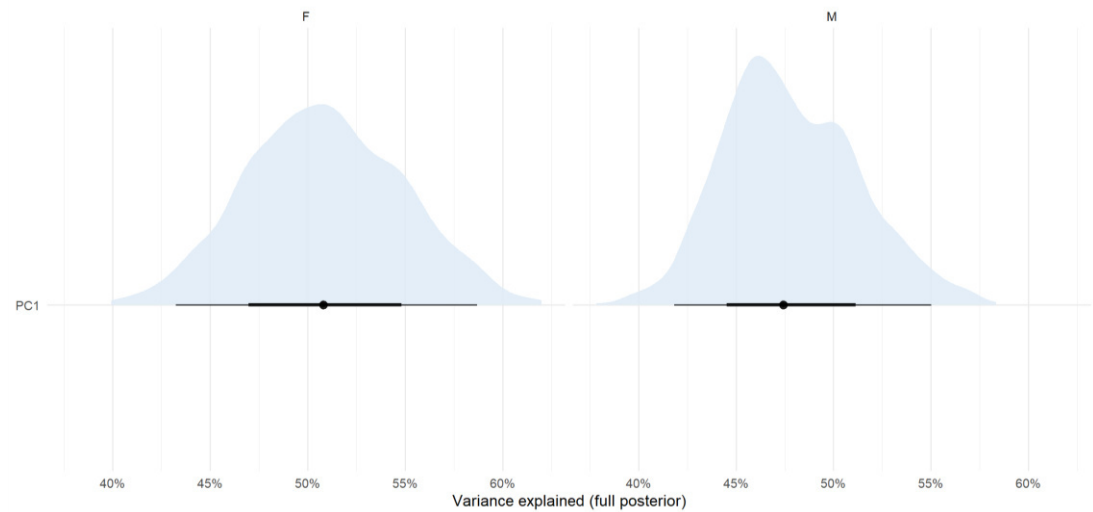


Figure 13. Full posterior PCA results by sex

The two panels show the full posterior distribution of the variance explained by the PC1 axis for each sex, calculated on 15 males and 12 females of Alpine chamois. Variance explained for females is shown in the left panel, whereas that for males is shown in the right panel. Slabs indicate the 89% and 50% credible intervals as thin and thick lines, respectively, with the point indicating the posterior mean.

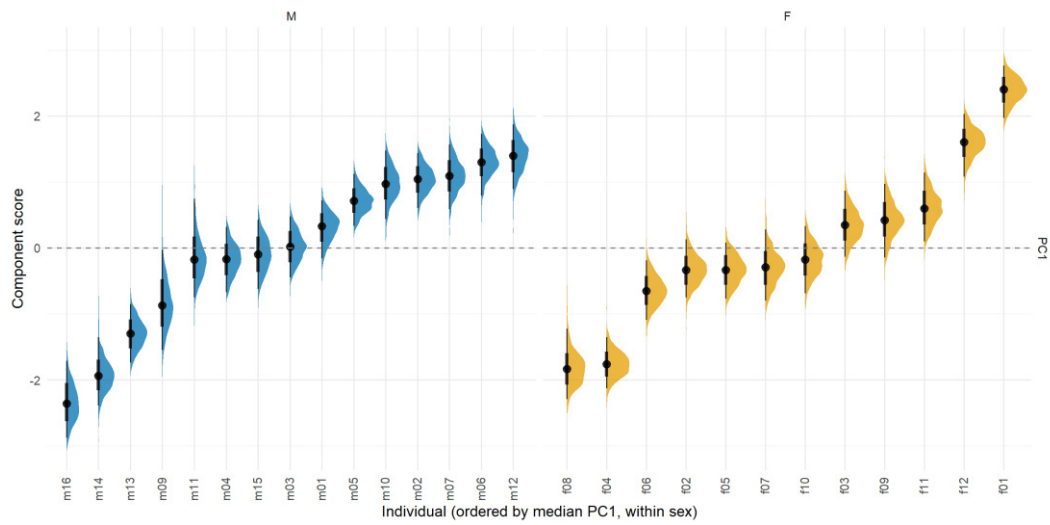


Figure 14. Individual scores on the PC1 axis by sex.

Full posterior distributions of the individual coordinates on the PC1 axis are shown. Slabs indicate the 89% and 50% credible intervals as thin and thick lines, respectively, with the point indicating the posterior mean. Female scores are shown on the left, whereas male scores are shown on the right.

3.3 Alignment between the axis and rut behaviour

Among the 14 males with rut data, coordinates on PC1 were credibly associated with *head-up* vigilance (posterior median Kendall $\tau = 0.30$ [0.10, 0.52]); the observed correlation posterior being clearly separated from the permutation null (KS $D = 0.70$). Associations with the other behaviours were weak and uncertain: *body-head shake* showed a weak positive tendency ($\tau = 0.19$ [-0.10, 0.45]) and *number females* a weak negative one ($\tau = -0.10$ [-0.41, 0.28]), the former differing from the null distribution ($D = 0.48$) and the latter not ($D = 0.20$). *Male-male interaction* ($\tau = -0.08$), *eating* (0.05), *resting* (0.01) and *scent-marking* (-0.01) all had τ near zero with credible intervals spanning zero (Figure 15).

The Spearman's rank correlation performed to assess the possible effect of age on male reproductive success detected no significant correlation in either 2024 ($\rho = -0.13$, $p = 0.65$) or 2025 ($\rho = -0.29$, $p = 0.36$). Therefore, the available data do not show any systematic variation in male chamois success with increasing age.

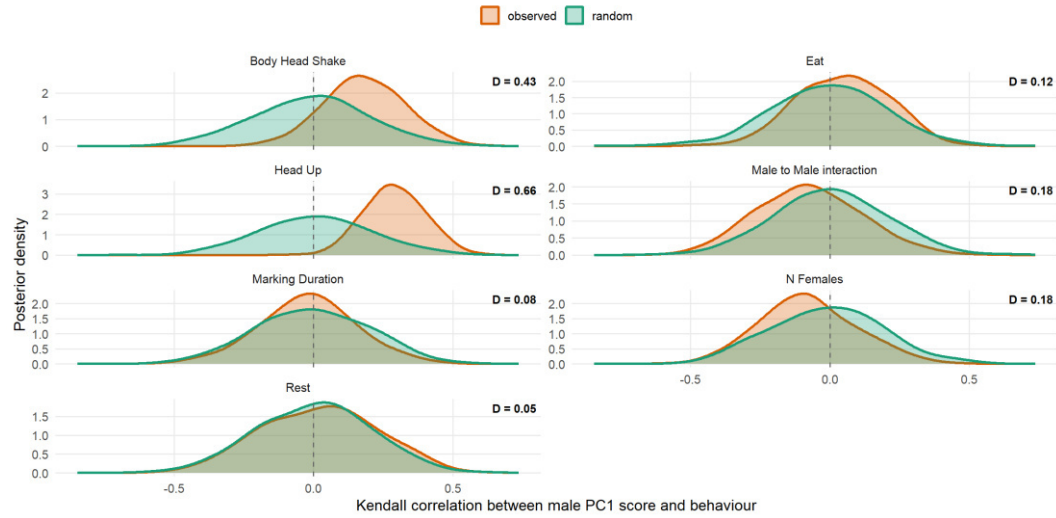


Figure 15. Kendall correlation results

Results of the Kendall correlation performed on the full posterior is displayed. Correlations were estimated from field observations collected from 14 male Alpine chamois during the reproductive periods (November–December) of 2024 and 2025. For further details on the selected behaviours, see Section 2.3.2 of the main text. Results were considered credible if the distance between vertices of the densities (D) of the observed vs the permuted (random) distributions were greater than 0.20.

4. DISCUSSION

The investigated behaviours showed different degrees of among-individual variation. Consistent inter-individual differences emerged for the three GPS-derived traits in both sexes, with risk-taking, activity, and exploration all exhibiting high variance across the population. Behaviours associated with reproductive performance showed clear among-individual variation for body-head shake and head-up vigilance, whereas weaker and more uncertain variations emerged for the other behaviours and the proxy of reproductive success, number of females.

The full-posterior PCA of the three movement related behaviours revealed in males a positive covariance among activity, risk-taking, and exploration, whereas in females, this covariance was positive only between activity and exploration, negative with risk-taking propensity.

This behavioural axis was found to be associated with male reproductive performance; among the behaviours considered, body-head shake and head-up showed the strongest correlations with the axis, positive for the former and negative for the latter, whereas the number of females exhibited only a weak negative correlation.

In line with hypothesis H1a, a consistently signed behavioural gradient was observed in males, along which more active individuals also tend to select less-recently-visited and higher-risk locations, indicating the existence of this behavioural syndrome in the male population during spring and summer.

This pattern is consistent with an among-individual boldness axis (Wilson et al. 2009; Michelangeli et al. 2019; Hughes et al. 2025), which has been documented across a wide range of taxa (Dingemanse et al. 2007), but has received little empirical support in chamois and, more generally, in wild large mammals.

Contrary, however, to the prediction of P1a, females only partially supported the investigated syndrome, as more active and exploratory individuals were found to be the most risk averse. Rather than being driven by the behavioural gradient, as predicted by P1b, the observed difference between sexes appears to stem from the covariation of activity levels and exploration with risk propensity, positive in males but negative in females.

Although unexpected, this result is consistent with the pronounced sexual behavioural dimorphism reported in chamois and other ungulate species, driven primarily by sex-specific differences in life-history strategies (Edelhoff et al. 2023). The need for males to accumulate energy reserves during summer for subsequent investment during the rut may underlie their pattern of risk propensity. In turn, the negative covariance with risk-taking observed in females is consistent with the trade-off they face, namely the need to safeguard the investment they have already made in their young (Wolf et al. 2007; Apollonio et al. 2020; Rees-Baylis et al. 2026).

The validation of this behavioural syndrome exclusively in males provides support for the assumption of the POLS hypothesis only in the male component of the population. Indeed, the finding that, in females, higher levels of activity and exploration are not associated with greater risk-taking, but rather with greater risk avoidance, does not fit well with the fast–slow continuum proposed by POLS (Réale et al. 2010; Royauté et al. 2018).

This discrepancy is, however, consistent with pronounced sex differences in reproductive success in chamois. Whereas males can potentially father from none to multiple offspring each year, females face a biological constraint on reproductive output, as they can produce only one kid per year. Therefore, repeated reproduction and offspring survival represent the only ways to increase their fitness (Krämer 1969, Corlatti et al. 2013). This could explain why, unlike males, females may not benefit from either a purely “fast” or a purely “slow” strategy. The greater risk propensity associated with a “fast” strategy could reduce their own long-term survival and, consequently, the number of reproductive seasons, whereas a “slow” strategy could entail lower resource acquisition and, in turn, reduced offspring survival.

In line with POLS predictions, in H2a I hypothesized that highly risk-prone, active, and explorative male chamois adopt a more capital breeding strategy. However, the limited variation in time spent feeding resulted in low repeatability of this behaviour, precluding a test of the association between the behavioural axis and the capital–income breeding strategy (Apollonio et al. 2020).

Based on the other rut behaviours investigated, it was possible to confirm an association between the behavioural syndrome and reproductive effort during the subsequent rut, as predicted according to H2b. The increase in the frequency of the behaviour body-head shake along the behavioural axis indeed demonstrated that males characterized by higher levels of risk-taking, activity and exploration during spring and summer are the same individuals that invest more time in agonistic behaviours, such as indirect aggression, during the rut (Corlatti et al. 2013). This finding is in line with the POLS theory (Réale et al., 2010) and

supports previous observations that individuals with a faster behavioural profile tend to be the most aggressive ones (Rudin et al. 2017; Wilson et al. 2009; Martorell-Barceló et al. 2023; Miguel et al. 2024; Garamszegi et al. 2009; Hertel et al. 2019).

The frequency of vigilance events was also associated with the syndrome axis, but in the opposite direction from that predicted by P2b, with faster males showing a higher frequency of head-up vigilance events during the rut. This behaviour is generally associated with more cautious individuals, which allocate more time to risk assessment (Welp et al. 2004). Thus, the most intuitive explanation for the higher levels observed in bolder individuals is that vigilance may serve an additional function during the rut, such as monitoring social dynamics, including tracking the movements of females and assessing potential competitors.

The number of females associated with each male (n females), used as a proxy for reproductive success, showed little inter-individual variation, as reflected by the low repeatability of this index. The hypothesized correlations in H2b between individual behavioural profiles and short-term reproductive success could therefore not be assessed.

Similarly, the other rut behaviours also showed insufficient variation among individuals to allow a clear assessment of their association with the behavioural syndrome.

Although some aspects could therefore not be fully assessed, the results nevertheless highlight the potential of the methodological approach adopted. First, an important innovation lies in the methodology used to identify the risk taking - activity - exploration behavioural syndrome, providing one of the first pieces of evidence that probabilistic model of movement decisions, based on Step Selection Functions (SSFs) (Thurfjell et al. 2014), is a biologically meaningful approach for characterising individual personality traits. Furthermore, combining these personality traits with behavioural data from field observations allowed behaviour to be investigated through two independent methodological approaches. This

proved to be an effective strategy, providing important biological insights into the assumptions and predictions of the POLS framework.

The main limitations that emerged from the analyses were related to the weak and uncertain inter-individual variation observed in several rut behaviours. This may be attributable to the limited statistical power of available data, which may have prevented the detection of clear differences among individuals. Increasing the number of observations per male and season would therefore represent an important step towards overcoming these statistical limitations.

In particular, the low repeatability in time spent feeding precluded testing the association between the behavioural axis and the capital–income breeding strategy. Likewise, the small differences in the number of females associated with each male (n females) made this proxy for reproductive success too weak to allow clear biological interpretations.

Regarding the latter, two main critical aspects emerge: its validity as a proxy for reproductive success and the extent to which the limited hours of observations available for each male and season are representative of its mating opportunities over the entire rut period.

To assess the reliability of this proxy for reproductive success, future cohorts of offspring should be genetically sampled to estimate the number of paternities assigned to each male and compare these values with the average number of females associated with each male during the rut.

Demonstrating the validity of this proxy is particularly important for advancing this type of research, given that, apart from genetic analyses, there are currently no alternative methods available for estimating male reproductive success in populations of large wild mammals.

More broadly, from a reproductive success perspective, the marked differences in behavioural patterns observed between males and females highlight the importance of considering sex-specific behavioural strategies. To further

investigate different behavioural trade-offs associated with sex, it would be valuable to extend reproductive success analyses to females. This could provide a broader and more robust analytical framework for assessing individual behavioural profiles from a life-history perspective, thereby offering an opportunity to further explore the limitations of POLS theory. However, this would require a long-term study, as several years of data are needed to detect differences in reproductive success among females (Rees-Baylis et al. 2026).

In conclusion, this study provides an interesting framework in which the methodological approach based on step selection functions (SSFs) was used to identify a behavioural syndrome in a population of large wild mammals, with this syndrome subsequently found to be associated with individual differences in male reproductive effort.

From a broader perspective, the results of this study highlight how the behavioural component at the individual level represents a key dimension of biodiversity within animal populations. This means that gaining a deeper understanding of the mechanisms that maintain behavioural diversity and its evolutionary implications is fundamental to assessing the resistance and resilience of wild large-mammal populations to rapid environmental changes and anthropogenic pressures (Wong et al. 2015). Human activities, like hunting, represent an important but often-ignored selective pressure on behavioural traits; they may drive exploitation-induced evolutionary changes that, in turn, could counteract adaptive responses to natural and sexual selection (Ciuti et al. 2012).

For these reasons, beyond its contribution to scientific knowledge, the in-depth study of behavioural ecology represents an essential element for managing animal populations through an increasingly integrated and conservation-oriented approach.

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