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Activity and space patterns of Pyrenean desman (*Galemys pyrenaicus*) suggest non-aggressive and non-territorial behaviour

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Abstract

The Pyrenean desman is considered as a flag species of biodiversity and evolution. However, its scientific knowledge is still under development and currently on debate, in special in relation to the behavioural ecology and social organization. Based on the previous hypothesis of individual desmans being solitary and territorial, activity and space patterns were described as arranged to avoid conspecifics. However, recent new insights into the species social behaviour revealed non-interspecific avoidance. With this study we provide novel insights into their activity and space patterns and their relation to the social behaviour. A total of 30 individuals were trapped of which 18 provided informative radiotracking data to study (1) individuals activity behaviour, (2) proportion of home range utilised and movement distances, and (3) movement directionality. Activity and space use patterns were affected by daylight and seasonality but not by sex, age or number of other conspecifics sharing the home range. In contrast to the previous observations, individuals did not show a pattern of directionally in their movements. Noticeably, we observed encounters between individuals without evidence of aggressive behaviour between them. Our results suggest that desmans do not opposite their activity neither their spatial behaviour in order to avoid encounters with conspecifics as previously suggested. These novel findings provide more evidences of a social structure and organization with social interactions and non-aggressive behaviour. This is of relevance for management actions and conservation purposes of this endemic mammal.

Authors declare no conflict of interest

Introduction

The Pyrenean desman (*Galemys pyrenaicus*; also known as Iberian desman) is a riparian species considered as a flag species of biodiversity and evolution because of its relic and narrow endemic character. Together with the Russian desman (*Desmana moschata*) represent the last two extant species of the Desmanini lineage of Soricomorpha (Nowak 1999) a mammalian taxa of extremely high biodiversity value. However, the species has been quite unknown to the general public due to its nocturnal elusive behaviour; and to the scientific community because the difficulty of its study (due to e.g. the few approved capture authorisations or the difficulty of scat identification using non-genetic methodologies since desman and shrew scats can easily be misidentified)

The first published information on its social and ecological behaviour was thanks to the novel studies carried by (Stone 1987b; Stone 1987a; Stone 1985; Stone and Gorman 1985), Stone (1987b; 1987a; 1985) in wild watercourses, and Richard and Michaud (1975) and Richard (1986; 1985) in captivity. Since then a few seminal studies have talked about its distribution, morphology and general biology (Aymerich and Gosàlbez 2013; Aymerich and Gosàlbez 2002; Bertrand 1993; Palomo et al. 2007; Queiroz and Almada 1993; Williams-Tripp et al. 2012) and most of them are grey literature and/or have low international repercussion. Nonetheless, in the recent years the interest on the species has increased notably by both the general public and the scientific community. Indeed, the Pyrenean desman recently became strictly protected under the Bern Convention (Appendix II) and the EU Habitats and Species Directive (Annexes II and IV). Notwithstanding, the scientific knowledge on its behaviour and ecology is still poorly developed.

One of the most unknown aspects of the species biology is its behavioural ecology and the reliability of little available information is currently on debate. The species was first observed as largely territorial and solitary or organised in couples in the wild (Stone 1987a;

Stone and Gorman 1985) and solitary in captivity (Richard and Viallard 1969). This hypothesis was supported by observations that described the individuals as highly aggressive with conspecifics independently of the sex even between couples, except for temporal mating and transient individuals (Stone 1987a). Since these first studies, there has been no more research on its social organization or behaviour, and these observations have been the foundation for the knowledge on the species behavioural ecology. Consequently, many studies were based on the aegis of desmans being aggressive with resident male and female couples occupying an exclusive range in which the male's range encloses that of the female, and individuals hold exclusive shelters (Richard and Valette Viallard 1969; Stone 1987b; Stone 1987a; Stone 1985). Controversially, we recently observed a different social behaviour with non-territoriality nor conspecific avoidance (Melero et al. 2012). More in detail, we found that socio-spatial organization was community based with non-exclusive or permanent territories and shared home ranges and resting sites (shelters used for more than 1h) between two or more resident non-couple individuals of different and/or same sex. Our new findings thus, recalled for a re-evaluation of the behavioural ecology of the species and the subsequent related research and management actions.

Under the observations of Stone (1985; 1987a;b) individual behaviour was observed to be arranged to avoid conspecifics. It was described as a bimodal activity rhythm with one diurnal and one nocturnal activity bout during which the whole riparian territory was seen to be patrolled on a 48h basis if solitary and 24h basis in the case of mating couples sharing the territory. In this patrolling, males were more frequently found in the border areas of the river sections included in their territories to protect the territory and mating couples avoiding encounters between them. In addition, individuals had fixed directional up or downstream movements that were organised between individuals to avoid encounters, including couples except for mating encounters. However, under the novel recent observations of the species not being territorial or aggressive (Melero et al. 2012), individual activity and space use might not follow the previously postulated objective of avoidance.

In this study, we investigated the activity and space use patterns of a local population of Pyrenean desman. We hypothesised that individual activity and space use patterns were not organised to avoid conspecific encounters. To test our hypothesis we studied (1) individuals activity behaviour (active versus inactive), (2) proportion of home range utilised and movement distances during the activity bouts, and (3) directionality of individual desmans. We also state several observed spatiotemporal encounters between individuals. Our overall aim was to increase the scarce research and knowledge on the behaviour of the species. We believe that clarifying the scientific knowledge on the species behaviour is crucial for the understanding of the species biology and its conservation. This will contribute to the awareness of the species and, ultimately, to improve design of on-going and future research, management and conservation actions.

Material and methods

The study area and the methodology for trapping and radiotracking was previously described in the in Melero et al. (2012) because the data used in this study was a subset of the data used in the preceding publication consisting of individuals captured between 2002 and 2004 in the river Tor.

Study area

The study was conducted in the river Tor, located in the Eastern Pyrenees (UTM 31TCH61). We selected 2 km of the river Tor which presented 4 m of mean width, 0.1-0.4 m of mean depth, and 6.5% of mean slope, rocky river-bed and rocky shorelines covered by dense vegetation. The river Tor is a well preserved river without anthropogenic pressures. Winter snowfalls and their subsequent spring thaws maintain a constant high river flow with a peak in April-May but without significant seasonal differences. Mean altitude of the area ranges between 1200 and 1400 m and precipitation falls regularly along the year within a range of 800-1000 mm being the highest between May and September. Temperatures in the area range from an average of 20 ºC in summer to -2 ºC in winter.

Other aquatic and semiaquatic vertebrates sharing the habitat with the Pyrenean desman are the brown trout *Salmo trutta*, viperine snake *Natrix Maura*, White-throated Dipper *Cinclus cinclus*, the Eurasian Water Shrew *Neomys fodiens*, the water vole *Arvicola sapidus* and the Eurasian otter *Lutra lutra*. The river provides availability of a diverse invertebrate fauna such as caddisflies (Trichoptera) and mayflies (ephemeroptera) among others.

Trapping and radiotracking

Two trapping sessions of 5 to 7 days each were conducted annually with 28-35 trap nights per session between 2002 and 2004. The sessions were set each year in April to June (spring-summer, spring hereafter) and in September-October (autumn) to cover both the expected reproductive and the non-reproductive seasons (Castién 1994). Animals were live trapped at night in partially submerged unbaited mesh traps designed for trapping the species and based on the designs of eel traps. Traps were located inside the rivers in adequate places for trapping (i.e. narrow pathways) maintaining a separation of 30-300 m between them and checked every 3 hours during the night every day (traps were open during daylight hours). After immobilization with anaesthetic (isoflurane), animals were measured, weighted, sexed, aged and classified as either a new capture or a recapture. Animals were classified by sex and age based on the data of Peyre (1961), González-Esteban et al. (2003) and González-Esteban et al. (2002) respectively. The captured animals were marked with a subcutaneous transponder (PIT; ID K162 FDX-B; AEG ID; Trovan Ltd., Madrid, Spain) and radiotransmitter (frequency 150-151, Pip model, BioTrack, Ltd., Wareham, Dorset, UK and Tinyloc Ltd., Mataró, Spain). Transponders weighted approximately 0.95mg < 1.7‰ of the lightest individuals (M16 and F11, weight = 54g). Radiotransmitters weighted approximately 2.5-3g < 5.5% of the weight of the lightest individuals and < 4.4% of the heaviest individual (F8, weight = 70g). All manipulated animals were released in the capture area once fully recovered. None of the captured individuals died during the procedures. Trapping was carried out by three accredited biologist and one accredited veterinary, but animal manipulation was carried out only by the accredited veterinary. Research permit and accreditations were provided by the Scientific Ethical Committee of the Department of Environment and Housing of the Catalonian Government (Spain). Our methods followed the "Guidelines for the Use of Animals in Research" (Association for the Study of Animal Behaviour and Animal Behavior Society 2012). All recaptured animals showed a good condition with no effects by the manipulation, the transponder or the transmitter. Failed radiotransmitters of recaptured individuals were removed following procedures explained above.

Radiotracking was done with a RX-8910HE (Televilt International AB) and three multidirectional and bidirectional antennas (for long, medium and short distances) with a mean precision of 0.2 and 0.1m respectively. Radiolocations were recorded by homing to the animals without triangulation as desman movements follow the river course. The study area did not have proper coverage for GPS systems. Therefore, animal position was recorded and mapped following as reference the 100 m signals of the road that flows parallel to the river (1 – 10m distance, mean = 7m). This and the narrow width of the river facilitated the location of the individuals with the precision of the bidirectional antennas being the limiting factor (0.1m).

Radiotracking was started five-seven days after the animal was released to avoid bias due to recovery from manipulation. Animal location was made daily; during night each individual was radiotracked every 1-2 h ($\bar{x} = 1.2$, SD = 0.3) when they were active and every 10-20 min when inactive to detect the re-start of the activity. During daylight radiotracking was made every 30-60 min. All individuals were tracked for 10-15min after located.

Activity patterns

Activity and inactivity behaviour was defined based on time spent outside (activity) or inside (inactivity) the resting site. Diurnal time was set between dawn and dusk for each day and nocturnal between dusk and dawn. Activity (n = 589) versus inactivity (n = 1024) was studied using only radiolocations separated at least 1h to reduce temporal autocorrelation except when individuals changed their behaviour leading to n = 559 and 977 respectively. The influence of sex, age, daylight (diurnal and nocturnal), season (spring-autumn) and number of conspecifics sharing the home range were analysed by means of generalised lineal mixed models (GLMM). Activity was fitted as to a binary distribution, and best model fit was selected based on AIC. Factors were set as fixed effects except for individual that was set as random effect. By considering individual as random effect, we tested individual variation and avoided the problem of different number of repeated measures per individual.

For conspecific sharing the territory that also had concurrently radiolocations we analysed if their frequencies of activity per hour were correlated with the activity of the other individual by means of a Pearson correlation. Overall, we had enough concurrently information for two pairs of individuals sharing the space: F1-F3 and M6-M15, and one pair of individuals captured together F10-M11. Radiotracking did not show space overlap between the pair F10-M11 but included it based on the fact that at some point the did share it.

Space use patterns

Space use was evaluated based on the home range use in terms of the percentage of the home range utilised during the individuals' daily activity as calculated as lineal meters of river section utilised. Home range size was obtained and exposed in our previously study (Melero et al. 2012). In relation to the movement patterns, we studied the distances travelled during the activity periods per day and the direction of the movement (upstream and downstream) using all radiolocations (n= 1613). Distance travelled per activity bout was defined as the sum of the distances from the resting site to the distal location points without counting sections travelled more than once (because e.g. of forward and backward movements). Percentage of home range used and direction of movement were set to binomial distributions, and distances travelled to a Gaussian distribution. All three variables were tested against the influence of sex, age, daylight (diurnal and nocturnal), season (spring-autumn) and number of conspecifics sharing the home range by means of GLMMs and linear mixed model (LMM) for distances travelled. We followed the same procedure as in the activity analyses for the fixed and random effects.

All models were fit in package lme4 and based on Restricted Maximum Likelihood (REML) and package lme done in R. Model selection was based on AIC criteria.

Results

We obtained the most completed radiotracking and trapping dataset up to date. A total of 30 individuals were trapped of which 18 provided enough radiotracking data to study their activity and home range (ten males and eight females). Individuals were tracked for at least 2 days and for a maximum of 33 days ($\check{x} = 25.3$, SD = 10.5; Table 1). The remaining individuals were not radiotracked due to transmitter failure before 2 days of radiotracking.

Activity pattern

On average, individuals spent more time inactive than active with 36.51% (SD = 23%) of active radiolocations, 9-10 h of activity per day. In general, the activity of desman was mainly nocturnal although the activity pattern differed between autumn and spring. During autumn, individuals presented two nocturnal, or exceptionally three, activity bouts with an average duration of 5 hours (SD = 1.5) each separated by one (exceptionality 2) inactive period of 100 minutes of average duration (SD = 57.81) commonly happening at 2pm approximately, and a single diurnal activity bout of 73.75 minutes of average (SD = 45.69; Fig. 1a). In spring, however, nocturnal activity was reduced to a single bout ($\check{x} = 8$h, SD = 1.6) without any inactive period but diurnal activity was longer ($\check{x} = 102$ min, SD = 52.51; Fig. 1b).

Best model fit included season and daylight but dismissed sex, age and number of conspecifics in the home range as factors influencing the activity pattern (in addition, in all models $p > 0.1$ for dismissed factors). Both season and daylight had a significant effect on activity ($F = 10.51$, $df = 1$, $p < 0.0001$ and $F = 2.61$, $df = 1$, $p = 0.009$ respectively) although their interaction was not significant (F = -0.25, $df = 3$, $p = 0.79$). Overall, individuals presented higher probability of being active at spring nights, followed by autumn nights; however, variability was also highest in them nocturnal spring activity (Fig. 2). Variance due to the random effect was low (7%) indicating low individual variability.

All cases where we had enough data on conspecifics sharing the territory showed a significant correlation between their frequencies of activity per hour. This correlation was high in the case of F1 and F3 ($r^2 = 0.83$, $df = 22$, $p < 0.0001$), and lower in the case of M6 and

M15 ($r^2 = 0.48$, $df = 18$, $p = 0.001$); similar to the pair trapped together F10 and M11 ($r^2 = 0.31$, $df = 21$, $p = 0.006$) (Fig. 3).

Space use pattern

Home range was almost completely utilised during their total nocturnal movements in autumn (average percentatge of utilisation $\bar{x} = 76.03\%$, SD = 24.09) with a slightly significant reduction in spring ($\bar{x} = 58.55\%$, SD = 17.10; $F = -2.65$, $df = 1$, $p = 0.01$; Fig. 4). During the daylight activity bouts home range was only partially utilised (11.6 % in autumn and 6.2 % in spring with not significant differences, $p > 0.1$; Fig. 4). Best model fit included season and daylight but dismissed sex, age and number of conspecifics in the home range as factors influencing the movement distances (in addition, in all models $p > 0.1$ for dismissed factors). There was no significant variability between individuals (variance due to random effect = 0.9%).

Distances travelled by the individuals at each activity bout were highest at night and in autumn (268.5 ± 123.9 m), with significant differences between seasons ($F = 13.77$, $df = 1$, $p < 0.0001$) and daylight ($F = 140.89$, $df = 1$, $p < 0.0001$; Fig. 5) but not with other factors. As before, best model fit all other factors (in all models $p > 0.07$ for dismissed factors). Variability due to individuals was again low (13%). During these displacement movements, individuals were observed to frequently travel from the resting site to the distal site of their home range and afterwards either rest in the same or different resting site or travel to the opposite distal point before resting. In relation to the direction of the movement, best model fit included all factors but there were no differences in the direction of the movement (up or downstream) for any of the models (all p-values > 0.4). Diurnal movements were always one way movement from the resting site and return to the same or, exceptionally, a different resting site. In all cases, individuals’ movement was straight forward, without forward and backward movements.

Spatio-temporal encounters

Several individuals were found to share the home range for 1- to 24- days (Table 1) and, of them the pairs F1 and F3, and M6 and M15 were both found together in the same location in eight occasions during six and three days of radiotracking respectively. In all the cases did not seem to alter their behaviour for conspecific avoidance. Encounters last from 10 seconds to up 10 min, but no longer than 5 minutes when all individuals were actively moving.

Discussion

This study provides evidence of the non-avoidance behaviour among individuals of Pyrenean desman. The individual activity and space use patterns of the studied population were not organised to avoid conspecifics. Indeed, we could directly observe encounters between individuals of different or same sex.

As previously described by Stone (1987b; 1987a), individuals presented a bimodal activity pattern in spring consisting of primary nocturnal activity bout ($\breve{x} = 8\text{h}$) of average and a short activity bout during daylight ($\breve{x} = 102\text{min}$). However, we observed a shift from this bimodal activity rhythm to a trimodal and exceptionally tetramodal in autumn. At this time individuals included 1 or 2 nocturnal resting bouts ($\breve{x} = 100\text{min}$) and reduced their diurnal activity to a single and shorter bout ($\breve{x} = 73.75\text{min}$) without resting time. This activity rhythm was never observed before, probably to the fact that Stone´s previous studies were always done in spring time. This shift in their rhythm is probably related to the individuals’ ability to adapt their behaviour to the duration of the night at different seasons.

Indeed, the only factors affecting their activity pattern were seasonality and daylight. It is possible that there is also relation between the duration of the diurnal and nocturnal activity and the biomass intake and/or the individuals' energetic requirements. The probability of activity during spring nights increased because there is not resting period and, thus, the probability of finding an individual active was higher, but the duration of the total nocturnal activity is shorter in spring when nights are also shorter than in the studied months of autumn. However, the duration of the diurnal activity bout increases in this spring, which might be related to a necessity of feeding to maintain its energetic requirements. Unfortunately, our data did not provide information to test this hypothesis.

Coinciding with Stone's previous studies, individual variation in the activity pattern was very low (7% variation due to individual effect) and independent of their sex, age and, more interesting of the number of conspecifics sharing the home range with them. These results support the previous hypothesis of a common activity pattern between individuals. In fact, for those cases sharing the home range where we had enough data, the activity of the individuals was significant correlated; information that, together with the model, supports the idea of a similar activity pattern between individuals.

In concordance with the observed activity pattern, seasonality and daylight were also the only factors influencing the range use and movement pattern of the studied population. In both cases, individual desmans utilised higher percentage of their home ranges and travelled longer distances at night and in autumn (76.03% versus 58.55% in spring nights). During the daylight activity bouts home range was only partial utilised (11.6 % in autumn and 6.2 % in spring with not significant differences, $p > 0.1$; Fig. 4). In addition, individual variation was again low (only 0.9% in the case of the home range use and 13% for travelled distances) which indicated a common pattern with independence of the sex, age or number of conspecifics sharing the home range. This findings, contradict the previous view that described their spatial behaviour based on sexual differences and conspecifics avoidance

(Stone 1987a; Stone 1985). Under the hypothesis of individuals being solitary and aggressive, the spatial behaviour of males and females was suggested to differ in order to maintain a mutual avoidance. This was based on the observations that the direction of the movements (upstream or downstream) seemed to differ between sexes which was explained as a pattern to avoid encounters with conspecifics occurring even in paired individuals (Stone 1987a; Stone 1985). In addition, males were observed to travel further distances than female while females mainly stayed in the neighbourhood of the resting site. Controversially, our results support a common spatial pattern for both females and males and a lack of mutual avoidance. Indeed, we observed no differences in the direction of the movement (up or downstream) between sexes, ages, daylight (diurnal and nocturnal), season (spring-autumn) or in relation to the number of conspecifics sharing the home range.

Our results indicate a general common behavioural pattern between individual desmans with a lack of mutual avoidance. This is supported by our previous findings were individuals on individuals concurrently sharing resting sites with independence of their sex or age (Melero et al. 2012). Activity and space patterns were previously explained based on the hypothesis of conspecific avoidance. However, our results suggest that individuals of Pyrenean desman do not organise their activity neither opposite their spatial behaviour in order to avoid encounters with conspecifics as previously suggested (Stone 1987b; Stone 1987a). Indeed, we could directly observe encounters with individuals without evidence of aggressive behaviour between them. The reasons for the differences between our studies and those by Stone are yet unknown. Differences in prey availability could be the first suggestion; however, there is not available data to test this hypothesis and both rivers seem to present similar resources and conditions. Notwithstanding, our current and previous findings are consistent with the behaviour of the most similar species, the Russian desman (Onufrenya and Onufrenya 1993). This species has similar ecological to the desman but it is considered a semi nomadic and non-territorial (Nowak 1999; Onufrenya and Onufrenya 1993) with social interactions between conspecifics.

Overall, based on our current observation and our previous study on the shelter use behaviour, we recall for a new understanding on the species behaviour based on a social organization hypothesis where individuals are non-aggressive neither territorial.

Management and conservation implications

Our findings are of significant relevance for management and conservation purposes of the species. The species distribution and status is currently being monitored by several national and international projects in Spain, France and Portugal (e.g. LIFE+ Desmania) mostly by means of indirect signs surveys consisting on annual scat surveys to map its distribution and potential expansion/contraction. In the past, the species distribution has also been mapped using other indirect signs that included not only scats but also interview to local residents. This type of information is, however, less reliable than the current methodology based on scat surveys. None of these methodologies allow identifying individuals and thus, estimating the density. Genetic monitoring using the collected scats will allow identifying individual. Until this is achieved, density estimations could be wrongly estimated if the surveys are based on the previous hypothesis. First, under the hypothesis of desmans being solitary and territorial, density has been calculated assuming a maximum of two (mating couple) individuals per mean home range (e.g. two individuals per 200-500m). However, based on our results there could be more than two individuals in the same home range length and thus, density would be underestimated. Estimation of population density based on presence absence data should be thus updated and used with criticism since until now they were done on the basis of individuals being in couples and maintaining fixed territories (e.g. Nores et al. 1998).

In addition, as observed in our previous study Melero et al. (2012) home ranges might not be fixed over the seasons and/or years. Thus, density could also be overestimated based when working with the hypothesis of fixed territories. Furthermore, this hypothesis of fixed territories can overestimate the species distribution, and connectivity between populations. This is due because, as with the density, distribution and connectivity are estimated based on presence absence data (direct captures or presence – absence of signs consisting mainly of scat surveys) assuming desmans do not change their territories. However, we have provided evidences of individuals with passing areas and temporal displaced home ranges.

Hence, we recommend population monitoring include shared territories and social interactions that allow more than two desmans per home range. In addition, based on our current and previous results (Melero et al. 2012) we also recommend to include the existence of passing areas and temporal home ranges (individuals changing the size and location of their home ranges) and to prioritize those river sections that are permanently occupied versus those temporally occupied.

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Table 1 Radiotracked individuals, number of tracked days and of radiolocations, season, percentage of active radiolocations, size of the home range (meters of river section),total number of conspecifics in their home range for 2- to 24- days and season Adapted from Melero el at. (2012).

Indiv.	Sex	Age at capture	No. of tracked days	No. radiolocations	Season	% active radiolocations	Home range (m)	Conspecifics in home range
F1	Female	Adult	25	111	Autumn	42.34	570	F3
F2	Female	Adult	21	126	Autumn	37.30	520	-
F3	Female	Adult	24	130	Autumn	41.54	430	F1
F4	Female	Adult	9	37	Autumn	35.13	530	M2*
F6	Female	Adult	8	64	Autumn	57.81	450	M5
F9	Female	Juvenile	3	11	Autumn	45.45	-	-
F10	Female	Juvenile	17	136	Spring	42.65	350	-
F11	Female	Adult	19	117	Autumn	19.66	660	-
M1	Male	Adult	34	206	Spring	34.95	530 – 2300†	-
M4	Male	Adult	20	112	Spring	40.18	620	F5*
M5	Male	Adult	2	6	Autumn	0	-	F6
M6	Male	Adult	33	232	Spring & Autumn	31.03	550-1350†	F7*, F8, M* M15
M7	Male	Adult	4	20	Spring	30	670	M10*, M12*, M8
M8	Male	Juvenile	16	134	Autumn	35.07	650	M10*, M12*, M7

M9	Male	Juvenile	3	4	Spring	0	-	-
M11	Male	Juvenile	7	48	Spring	41.67	320	-
M15	Male	Adult	7	37	Autumn	37.83	450	M6
M16	Male	Adult	8	75	Autumn	37.33	510	-

*marked individuals that did not provide enough information for the analyses.

[†] Outliers due to exceptional one day long movements. Outliers were not taken into account in the analyses.

Figure 1 Percentage and standard error of activity per hour of the studied population of Pyrenean desman in (a) autumn (n = 994) and (b) spring (n = 669) seasons. Data was gathered by means of radiolocation.

Figure 2 Estimated probability of being active for the studied population of Pyrenean accordingly to daylight (diurnal and nocturnal) and season (autumn and spring). Values are given as mean and their standard error calculated from the GLMM.

Figure 3 Estimated activity correlation between pairs of the studied population of Pyrenean desman F3-F1, M15-M6 and F10-M11. Values are given as between percentage of active radiolocations per hour (%). Dotted lines stand for the estimated correlation.

Figure 4 Estimated percentage of home range utilised of the studied population of Pyrenean desman accordingly to daylight (diurnal and nocturnal) and season (autumn and spring). Values are given as mean and their standard error calculated from the GLMM.

Figure 5 Estimated total distance travelled during the activity bouts of the studied population of Pyrenean desman accordingly to daylight (diurnal and nocturnal) and season (autumn and spring). Values are given as mean and their standard error calculated from the GLMM.