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Need for speed: Preference for fast-flowing water by the endangered semi-aquatic Pyrenean desman (*Galemys pyrenaicus*) in two contrasting streams

Amaiur Esnaola[1] | Jorge González-Esteban[2] | Arturo Elosegi[3] |
Aitor Arrizabalaga-Escudero[1] | Joxerra Aihartza[1]

[1] Department of Zoology and Animal Cell Biology, University of The Basque Country UPV/EHU, Leioa, the Basque Country, Spain

[2] DESMA Estudios Ambientales, Sunbila, Navarre, Spain

[3] Department of Plant Biology and Ecology, University of The Basque Country UPV/EHU, Leioa, the Basque Country, Spain

Correspondence
Joxerra Aihartza, Department of Zoology and Animal Cell Biology, University of the Basque Country UPV/EHU, Sarriena s.n., E-49840 Leioa, the Basque Country, Spain.
Email: joxerra.aihartza@ehu.eus

Abstract

1. The Pyrenean desman (*Galemys pyrenaicus*) is an endangered, semi-aquatic, insectivore mammal, endemic to the northern Iberian Peninsula and the Pyrenees. Owing to its small populations, evasive behaviour, and nocturnal activity, knowledge of its ecological requirements is still limited. Continuing population decline over most of its distribution range – even in regions where water quality has clearly improved – points to other factors as the main conservation threat. Nevertheless, at present there is a lack of information on its habitat preferences within its area of occupancy (e.g. stream microhabitat characteristics), a key point for assessing or improving its habitat.

2. This study used radio-telemetry data to determine the use of space at microhabitat level by the desman, and how this changed depending upon environmental conditions.

3. Desmans were studied in two contrasting rivers in the Basque Country (northern Iberian Peninsula): Elama, a nearly pristine stream, and the Leitzaran, a clean-water stream affected by hydropower diversions. Fifteen desmans were captured and radio-tracked in Elama and 16 were captured and radio-tracked in the Leitzaran, and nocturnal activity points were assigned to one of three habitat types: riffles, runs, or pools. Habitat use was compared against availability to measure habitat selection in each stream and between streams.

4. Desmans selected riffles positively and pools negatively, with this selection being stronger in the Leitzaran.

5. The results highlight the ecological relevance of riffles as foraging habitats of desmans, and therefore as key features for their conservation. It suggests that channel modifications that reduce the areal cover of riffles impair habitat quality for this species. In addition, water diversion for hydropower is likely to be detrimental for desmans, as it reduces discharge and flow velocity in the bypassed river sections.

KEYWORDS

behaviour, endangered species, habitat management, hydropower, mammals, river, stream

1 | INTRODUCTION

The Pyrenean desman *Galemys pyrenaicus* (Geoffroy, 1811; Figure 1) is an endangered semi-aquatic mammal endemic to the northern Iberian Peninsula and the Pyrenees (Palmerin & Hoffman, 1983), specialized for life in cold streams, with paddle-like hind feet and a long and laterally compressed tail, adapted to swimming and diving (Richard, 1986). The Pyrenean desman is protected under the Bern Convention (Appendix II) and the European Habitats Directive (Annexes II and IV) (Council of the European Communities, 1992). Its distribution area has been severely reduced during recent decades, and it is currently listed as a vulnerable species in the Red List categories by the

FIGURE 1 The Pyrenean desman (*Galemys pyrenaicus*) in the Elama Stream. Photo by Jorge González-Esteban

International Union for Conservation of Nature (IUCN) (Fernandes, Herrero, Aulagnier, & Amori, 2008). The reasons behind this decline are not well known, but seem to be mainly linked to anthropogenic factors such as water pollution, habitat degradation (canalization, river-bank degradation, flow modification), and stream fragmentation (Charbonnel et al., 2016; Queiroz, Bertrand, & Gennady, 1996; Williams-Tripp et al., 2012). It must be noted that the population decline occurs even in regions such as the Basque Country (Ihobe, 2011; Rubio, 2016; Ura, 2017), where pollution has abated as a consequence of improved sanitation and water-treatment schemes. This suggests that there are other potential factors causing the decline, among which the degradation of physical habitat stands out.

Desmans typically use home ranges of several hundred metres in length, and tend to have a bimodal activity rhythm, with one short bout of diurnal activity and one principal bout of nocturnal activity (Stone, 1985, 1987). The night foraging pattern in turn shows two or three activity peaks (Melero, Aymerich, Santulli, & Gosàlbez, 2014). It is unclear whether the desman demonstrates territorial behaviour and whether individuals share shelters independently of sex, age, or number of conspecifics sharing the home range (Melero, Aymerich, Luque-Larena, & Gosàlbez, 2012). Desmans usually shelter in natural crevices between rocks, in stone walls, or below the roots of riparian trees; usually there are no outwardly visible signs of the shelters from the surface (Stone, 1987). They feed mainly on freshwater invertebrates (Biffi et al., 2016; Santamarina & Guitian, 1988). Many factors can affect freshwater invertebrate abundance and composition, from pollution to drought, or changes in physical habitat (Cowx, Young, & Hellawell, 1984; McIntosh, Benbow, & Burky, 2002; Wood, Agnew, & Petts, 2000). Invertebrates typically have a patchy distribution in rivers, with their composition and abundance differing between habitat types such as riffles, runs, and pools (Dewson, James, & Death, 2007), as well as depending on sediment grain size (Elosegi, Flores, & Díez, 2011). Therefore, freshwater invertebrate abundance and diversity can decrease as a consequence of stressors such as water diversion (McIntosh et al., 2002).

Charbonnel et al. (2015) suggested a positive influence of stream flow and substrate heterogeneity on desman occupancy, based on occupancy models applied in one French Pyrenean catchment. Desmans seem to be rheophilic, i.e. have a strong preference for fast-flowing waters, which we here call a 'need for speed'. Charbonnel et al. (2015) hypothesized that this preference is caused by a higher abundance and richness of invertebrates in fast-flowing reaches,

whereas Richard (1986) explained it mechanically, arguing that high water velocity may help the animal to counteract its natural buoyancy. Morueta-Holme, Fløjgaard, and Svenning (2010) highlighted the importance of discharge, as more water offers better habitat conditions and greater food availability. Biffi et al. (2016) provided information about habitat factors measured at the local scale in river stretches occupied by desmans, but did not provide information about factors controlling occupancy at the microhabitat scale: key information for understanding the needs of desman. Moreover, as habitat selection patterns change spatially according to differences in habitat availability (Ayllón, Almodóvar, Nicola, & Elvira, 2010; Boyce et al., 2016), it is necessary to study the behavioural response of desmans in contrasting environments to understand better the key factors shaping their habitat preferences. Most of the studies have coarse spatial resolutions, because environmental data have not been calculated in the field. In addition, almost all habitat studies for the Pyrenean desman have been based on stool detections as signs of presence (Barbosa, Real, & Vargas, 2009; Charbonnel et al., 2015, 2016; Morueta-Holme et al., 2010; Williams-Tripp et al., 2012). None of these studies have been made using telemetry data, which could give new relevant information for individual identification and the tracking of displacements.

The aim of this study was to determine the foraging habitat preferences of the Pyrenean desman within its home range to identify factors affecting its habitat suitability. It was hypothesized that: (i) desmans prefer riffles, which are more productive in terms of prey availability (Dewson et al., 2007) and are easier for foraging by a buoyant predator; and (ii) habitat preference patterns, or intensity of habitat selection, change with stream characteristics. Therefore, this study was carried out in two contrasting streams: the Elama, a nearly pristine stream, and the Leitzaran, a stream affected by water diversions for hydropower.

2 | METHODS

2.1 | Study area

The study was conducted in two mountain streams in the northern Iberian Peninsula (in the Basque Country; Figure 2). Both study sites are protected within the European Union Natura 2000 network (Council of the European Communities, 1992), and both are at good ecological status according to the European Water Framework Directive (Council of the European Communities, 2000), but contrast in the environmental pressures that they experience. The Elama (Figure 3) is a second-order headwater stream draining an uninhabited basin of 1415 ha over granite and schist that has been managed strictly as a nature reserve since 1919, resulting in extensive cover of beech and oak forests (Castro, 2009). At present there is no extractive activity in the Elama basin. On the other hand, the Leitzaran (Figure 4) is a fourth-order stream draining a basin of 12 402 ha over limestone, slate, and sandstones. Contrasting with Elama, in the headwaters of Leitzaran there are two towns totalling 3150 inhabitants, but then the stream enters a long, uninhabited valley approximately 25 km in length where forestry and hydropower diversion schemes are the main human activities (Izagirre, Argerich, Martí, & Elosegi, 2013). The
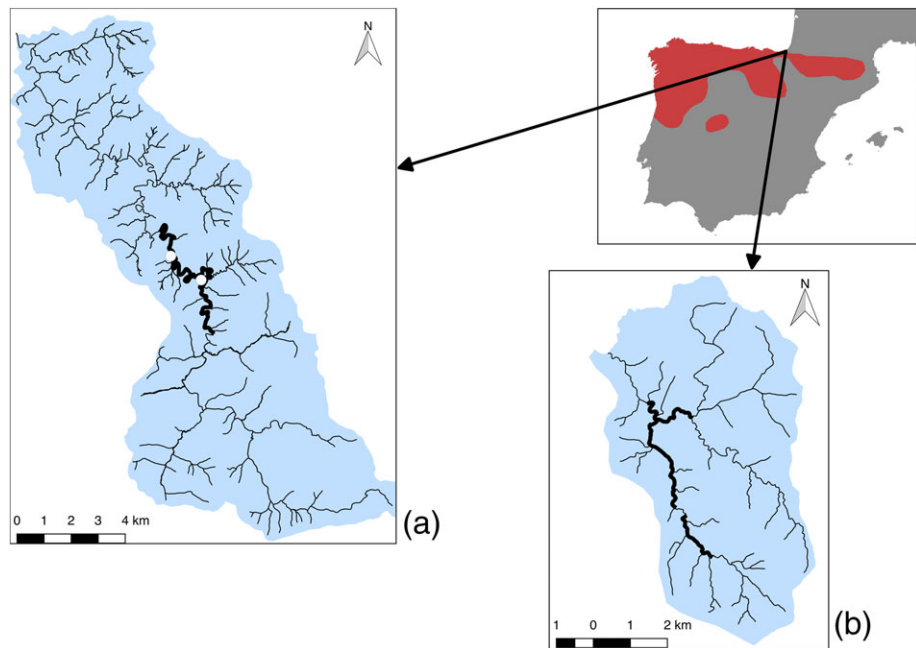
FIGURE 2   Study area: (a) Leitzaran and (b) Elama streams in their basins. The study section of each stream has been depicted with bolder black lines. The white dots mark the dams present in the study sections. The distribution of the Pyrenean desman in the Iberian Peninsula has been represented in red (Fernandes et al., 2008)
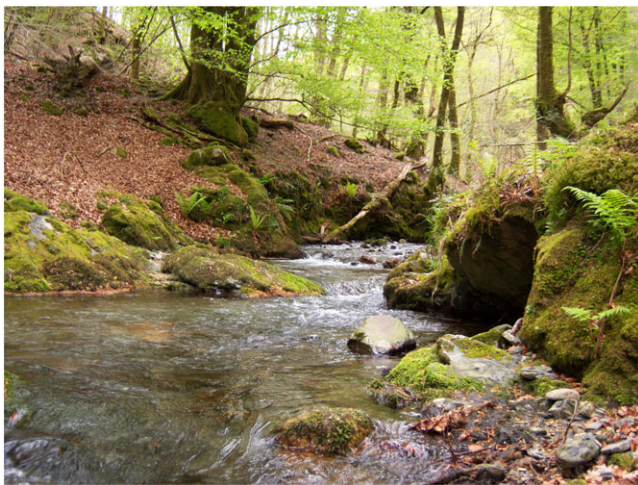

FIGURE 3   The Elama Stream, Basque Country. Photo by Amaiur Esnaola

hydropower diversion schemes consist of low weirs (2–4 m in height) that divert water from the stream channel to diversion canals several km long, and lead to hydraulic turbines before returning the water to the stream. The storage capacity of the reservoirs above the weirs is very small, but the proportion of water diverted is high. Most hydropower concessions must leave an environmental flow, which is usually set at 10% of the average flow calculated for each month (Boletín Oficial del Estado (BOE), 2016). Nevertheless, some old concessions still have no environmental flow requirements, and thus practically dry out entire stream sections. Hydropower plants in the area tend to operate throughout most of the year, stopping only in summer or early autumn for maintenance operations, or when the water authorities compel them to ensure environmental flows (Iñaki Bañares, Province Government of Gipuzkoa, pers. comm., September 2017).

Hydropower schemes are typically set in close succession, with diversion weirs being located almost immediately below the outflow from hydropower turbines. Therefore, in streams affected by hydropower, the bypassed sections are much more abundant than sections with natural discharge. In the mid- and low-Leitzaran stream, over 70% of the main-stem channel length is bypassed by diversion canals, and an additional 4% is converted into slow-flowing areas above weirs (Izagirre et al., 2013).

The research was carried out on a 4-km section of the Elama Stream (from 43°12′40″N, 1°48′36″W to 43°11′14″N, 1°48′4″W; mean altitude, 330 m; mean width 7.08 m), and on a 10-km section of the Leitzaran Stream (from 43°8′57″N, 1°57′26″W to 43°6′55″N, 1°56′9″W; mean altitude, 290 m; mean width, 12.42 m) (Figure 2). The section lengths were different because of the greater difficulty in trapping desmans in the Leitzaran Stream.

2.2 | Habitat availability and characteristics

Both streams were surveyed in September and October 2016 by walking the entire sections with the aid of a GPS and topographic maps. Three habitat types were identified, following Overton, Wollrab, Roberts, and Radko (1997): riffles with fast, turbulent water, uneven surface level, and white water; runs with close to laminar flow and even depth; and pools with slow flow on riverbed depressions.

Each stream section was divided into subsections according to the dominant habitat type: riffle, run, or pool. Boundaries of habitat types were recognized by identifying the breaks in stream channel slope along the thalweg of the channel bottom. Each habitat type was characterized by 10 transversal transects conducted for each section. More precisely, in each transect the wetted width was measured, and at regular intervals (0.5 m in the Elama; 1 m in the Leitzaran) the depth and water velocity at 0.6 of maximum depth (current meter Martin Marten
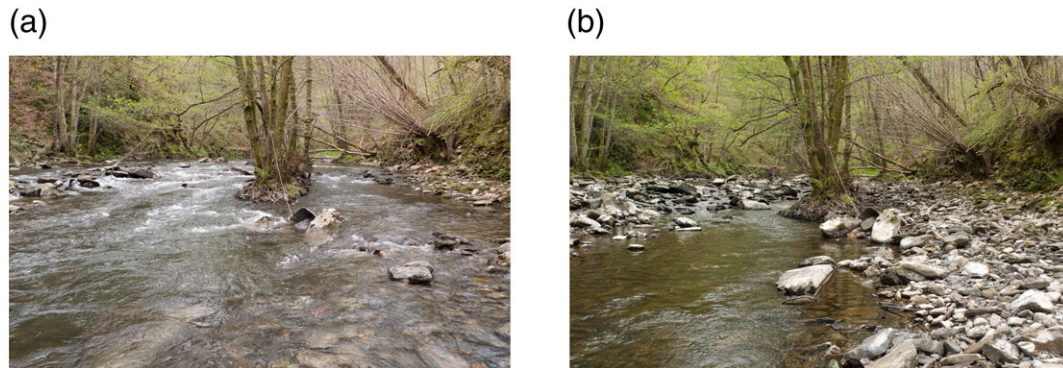
FIGURE 4 The Leitzaran Stream, Basque Country: (a) a stream stretch occupied by desmans with its natural flow (21 April 2016); (b) the same stream stretch 5 days later (25 April 2016), when a hydroelectric plant diverted most of the discharge. The contrast of both images shows the effect that water diversion has on the distribution of hydromorphological habitats, especially the reduction of both total wetted area and riffle area. Photos by Jorge González-Esteban

Z30, Barcelona, Spain) were measured. Substrate was also characterized by visually assigning the bottom to size categories: sand, gravel, pebble, cobble, boulder, and others (rock, bedrock, or organic) (Díez, Larrañaga, Elosegi, & Pozo, 2000). In these surveys, the study sections were marked with plastic tape every 25 m to improve the GPS location.

2.3 | Desman capture and tracking

This research was performed outside of the desman mating and breeding season (from January to August; Palmerin & Hoffman, 1983) to avoid disturbing pregnant females or females with cubs. Desmans were captured in September and October 2016 using wire-mesh traps placed partially submerged in the streams during the night, and checked every 3 h to minimize stress (González-Esteban, Villate, & Castién, 2003a). Two trapping sessions were carried out in each stream, with 12 traps used per night, and with each trapping session lasting two or three nights. Captures were less frequent in the Leitzaran, where a greater trapping effort was required to capture a similar number of individuals (four capture nights in the Elama versus six capture nights in the Leitzaran).

The age and sex of captured desmans were determined visually (González-Esteban, Villate, & Castién, 2003b; González-Esteban, Villate, Castién, Rey, & Gosálbez, 2002), the hair on their back (approximately 1 cm^2) was trimmed with scissors, radio-transmitters (0.75 g in weight, model A2435, Advanced Telemetry Systems, https://atstrack.com) were glued with Dermabond™® and animals were set free where they were captured. The process typically lasted 15–20 min per animal.

Tagged desmans were tracked for five nights, as a compromise in order to obtain enough information about the activity of each individual in the shortest possible time. This also prevented the radio-transmitters from falling off and avoided the occurrence of major environmental changes (such as strong weather disturbances) during the tracking period, which could distort the results. Radio-tracking was carried out on foot using two types of radio receivers and antennae (TRX1000S, Wildlife Materials Inc., Carbondale, IL, USA, with hand-held three-element Yagi antennae; AOR AR8200 Mark III B, Universal Radio Inc., OH, USA, with H-type antenna). Desmans were tracked as close as possible to identify their activity overnight. Periods

of activity and rest were distinguished from the variations in radio signal. To minimize spatial autocorrelation, successive position recordings, i.e. fixes, were taken at least 5 min apart, as in that time each individual could reach any habitat type (Stone, 1987). Resting locations were later excluded from the analysis.

Desman capture and handling protocols met the guidelines for treatment of animals in research and teaching (Animal Behaviour Society, 2012). The study met local legal requirements and was approved by the Ethics Committee for Animal Welfare of the University of the Basque Country (ref. CEBA/M20/2016/022).

2.4 | Data analysis

Habitat information and radio-tracking fixes were transferred to a GIS system (ArcView 3.2; ESRI, Redlands, CA, USA). Individual habitat availability and home range (length in m, area in m^2) were determined, calculating preferential foraging areas with the Animal Movement 2.0.β extension for ArcView 3.2 (Hooge & Eichenlaub, 1999), considering only active locations. Preferential foraging areas were determined by kernel home ranges (Kernel Density Estimation (KDE) 95%), which are based on the probability of use derived from the number and spatial arrangement of locations, and the relative length of time an animal spends in a given area (Worton, 1989). Kernels were calculated by the fixed kernel method and the smoothing factor was estimated by means of least-squares cross-validation. Differences in home ranges (KDE95%; in length and in area) and in available riffle, run, and pool areas (from KDE95%) between study sites were tested statistically with the nonparametric Mann–Whitney U-test.

Independence among habitat availability and use was tested with χ^2 goodness-of-fit (log-likelihood ratio G). Habitat types were ranked in order of relative preference according to their average selection ratio w_i (Manly, McDonald, Thomas, Mcdonald, & Erickson, 2002): the average of the ratios of the observed proportion of each habitat type used by each animal to the known proportion of each habitat type available to the population, for the whole population of animals in each stream. To assess the selection or rejection of a given class of habitat, Bonferroni's confidence intervals were constructed, following Manly et al. (2002), to estimate habitat availability and use individually. Comparisons between streams were made using the average selection

ratios, taking into account Bonferroni's confidence intervals. For all tests, α was set to 0.05 corrected by the number of simultaneous comparisons. The confidence intervals were computed at the 95% level, also corrected by the number of simultaneous comparisons. Individual selection was represented by one habitat selection diagram for each stream (SOILTEXTURE package in R).

3 | RESULTS

3.1 | Habitat availability and characteristics

In the Elama, riffles and runs were similarly available (proportions of 0.48 and 0.49, respectively; Table 1), whereas runs dominated the Leitzaran (0.62; Table 1). Pools were the least abundant habitat in both streams (0.03 in the Elama, 0.11 in the Leitzaran; Table 1). In general, riffles were slightly narrower, considerably shallower, and much faster than runs and pools. Water depth was in general greater in the Leitzaran, whereas overall differences in water velocity among streams were small. In the Elama, boulders prevailed in riffles, cobbles in runs, and other types of substrates prevailed in pools. In the Leitzaran, boulders dominated in riffles and runs, and other types of substrates dominated in pools.

3.2 | Captures

Thirty-one desmans were captured and successfully tracked: seven female and eight male desmans in the Elama, and 10 females and six males in the Leitzaran (Table 2).

3.3 | Home range size and habitat selection

Overall, more than 200 activity points were recorded for each individual, and animals were followed for more than four nights (Figure 5; Table 2). Length of home ranges (KDE95%) did not differ significantly between streams (length of individual foraging area, LIFA; $w = 135$, $P = 0.5665$), but their area was significantly larger in the Leitzaran than in the Elama (area of individual foraging area, AIFA; $w = 26$, $P < 0.0001$; Table 2). Although riffles covered a smaller proportion of the stream channel in the Leitzaran, the total area of riffles within home ranges was higher there (KDE95%; $w = 29$, $P = 0.0003$; Table 2), as well as the total area of runs (KDE95%; $w = 63$, $P = 0.0255$; Table 2), because this stream was significantly larger. There were no significant differences between the total area of pools (KDE95%; $w = 109$, $P = 0.6663$; Table 2).

In the Elama, 63.7% of the active locations were recorded in riffles, 33.1% in runs, and only 3.2% in pools (Table 3). Riffles were used disproportionately to their availability (i.e. there was positive habitat selection; $\chi^2 = 361.2$, d.f. = 30, $P < 0.0001$) and runs were selected against, whereas the data were not statistically significant for pools (Table 3). In the Elama, one desman did not follow this general pattern and positively selected pools instead (Figure 6).

In the Leitzaran, 83.7% of the active locations were recorded in riffles, 14.8% in runs, and 1.5% in pools. Riffles were selected positively ($\chi^2 = 819.9$, d.f. = 32, $P < 0.0001$), and runs and pools were selected negatively (Figure 6; Table 3). Overall, habitat selection was stronger in the Leitzaran than in the Elama, as shown by a higher

TABLE 1 Habitat characteristics in the Elama and Leitzaran streams

Stream	Habitat	Availability	Channel width (m) mean ± SD	Depth (cm) mean ± SD	Water velocity (m s⁻¹) mean ± SD	Sand (%) ± SD	Gravel (%) ± SD	Pebble (%) ± SD	Cobble (%) ± SD	Boulder (%) ± SD	Other (%) ± SD
Elama	Riffle	0.48	6.7 ± 2.4	9.13 ± 2.78	0.31 ± 0.13	0.8 ± 2.6	5.7 ± 8.1	10.1 ± 10.1	28.5 ± 20.3	32.6 ± 20.6	22.2 ± 29.8
	Run	0.49	7.4 ± 1.3	16.79 ± 4.10	0.09 ± 0.03	6.7 ± 9.7	18.6 ± 13.2	19.0 ± 15.8	29.6 ± 13.2	21.8 ± 16.7	4.3 ± 6.6
	Pool	0.03	7.1 ± 2.8	57.74 ± 16.59	0.03 ± 0.02	18.6 ± 15.8	9.4 ± 8.6	12.4 ± 10.9	14.3 ± 16.1	14.3 ± 11.7	31.0 ± 19.4
Leitzaran	Riffle	0.27	11.5 ± 2.8	11.28 ± 2.81	0.36 ± 0.11	0	2.5 ± 7.9	0	25.1 ± 9.1	65.3 ± 14.5	7.1 ± 12.8
	Run	0.62	12.1 ± 2.0	28.86 ± 9.95	0.07 ± 0.04	5.6 ± 9.1	12.0 ± 10.2	5.7 ± 8.9	20.3 ± 21.6	34.7 ± 28.6	21.6 ± 23.7
	Pool	0.11	13.6 ± 4.7	73.56 ± 27.01	0.02 ± 0.02	2.5 ± 4.3	12.9 ± 10.7	7.7 ± 9.6	19.1 ± 21.1	14.1 ± 13.9	43.6 ± 27.5

'Availability' shows the proportion of each habitat type in the entire study section of each stream.

TABLE 2 Details of animals followed in the Elama and Leitzaran streams

Stream	Desman capture nights	Tracked desmans	Females	Males	Active location points mean ± SD	Tracking nights mean ± SD	LIFA (m) (KDE95%) mean ± SD	AIFA (m²) (KDE95%) mean ± SD	Riffle area (m²) (KDE95%) mean ± SD	Run area (m²) (KDE95%) mean ± SD	Pool area (m²) (KDE95%) mean ± SD
Elama	4	15	7	8	268.9 ± 44.9	4.73 ± 0.57	328 ± 72	2215.6 ± 345.3	1103.3 ± 394.7	1038.7 ± 494.0	73.6 ± 78.6
Leitzaran	6	16	10	6	200.4 ± 32.9	4.19 ± 0.83	368 ± 231	6176.9 ± 5201.9	2379.3 ± 1298.1	3295.2 ± 3497.8	502.5 ± 761.9

LIFA (KDE95%), length (m) of individual foraging area (kernel 95%); AIFA (KDE95%), area (m²) of individual foraging area (kernel 95%). Available riffle, run, and pool mean areas (kernel 95%) are also included.

average selection ratio (1.70 versus 1.26) and a greater distance between the pink and green dots in Figure 6.

While out of their burrows, desman movements showed uneven patterns. Commonly, individuals ranged every night along a stretch of a few hundred metres in length, concentrating their foraging activity for several minutes in specific areas (generally riffles), before moving on to the next foraging spot. However, some animals moved swiftly some hundreds of metres from the nest to a riffle in a few minutes, and then remained there for 1–3 h. In those 'hot spots', changes in the intensity of radio signals suggested constant movement but restricted to a few metres. The long stays happened especially in riffles where the stream channel branched and where there were large boulders or fallen logs, which trapped branches and leaf litter.

4 | DISCUSSION

The present research shows the Pyrenean desman to select riffles positively and pools negatively. It also shows that the intensity of habitat selection changes among streams, with selectivity being higher in the stream that was affected by hydropower schemes. These results add valuable information on the factors likely to affect desman habitat quality, and on potential management actions for improving the conservation status of this endangered mammal.

Human pressures such as habitat destruction and water pollution are blamed for the population decline of the Pyrenean desman (Queiroz et al., 1996; International Union for Conservation of Nature (IUCN), 1995). In particular, local extinctions have been attributed to artificial barriers to dispersal, such as dams or highly altered reaches in a dendritic network where biogeographic barriers already abound (Morueta-Holme et al., 2010). Comparing the historical with the present distributions of the species in France, Charbonnel et al. (2016) concluded that the range contraction observed is larger than expected from the decrease in habitat suitability caused by climate, and hydrological and land-use changes. They speculated that the decline may be caused by additional factors such as habitat fragmentation, pollution, changes in prey availability, or invasive species (e.g. the American mink *Neovison vison*) preying on the desman, but gave no suggestions on the relative importance of this list of potential factors. Therefore, this list is still too generic a foundation for conservation, which is reflected in the paucity of conservation actions tailored to the desman. As an example, both the French Conservation Action Plan for the Pyrenean Desman (Némoz & Bertrand, 2008) and the Spanish Desman Conservation Strategy (Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA), 2013) include a wealth of actions on research and science, but almost no specific actions devoted to habitat improvement.

Stream flow velocity has been reported as an important environmental factor for the Pyrenean desman (Charbonnel et al., 2015). Biffi et al. (2016) performed an Ecological Niche Factor Analisys (ENFA) based on the detection of faeces. They concluded that the habitat of the Pyrenean desman is characterized by in-stream variables (substrate heterogeneity, fast-flowing water, absence of fine sediment), as well as by bank characteristics (rocky banks), with desmans preferring sites with abundant emergent structures and a high heterogeneity of
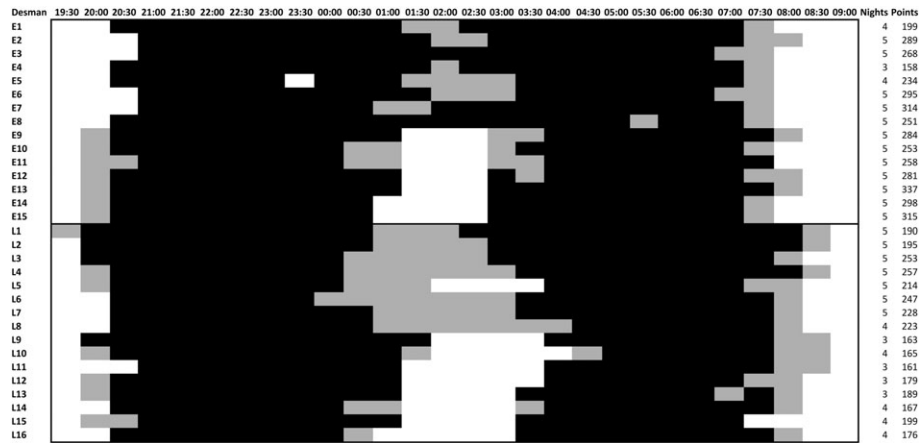
FIGURE 5 Periods of time each animal was radio-tracked during the night: black areas represent activity periods, grey areas represent inactivity periods, and white areas show radio-tracking lapses. The codes in the 'Desman' column refer to individual animals in the two streams (E, Elama; L, Leitzaran). The number of tracking nights that each animal has been followed ('Nights') and the number of active location points recorded for each individual ('Points') are also indicated in columns on the right

TABLE 3 Habitat use, Bonferroni's confidence intervals of habitat use, habitat availability, and average selection ratio (Manly et al., 2002) in the Elama and Leitzaran streams

Stream	Microhabitat	Habitat use u_i	Bonferroni's confidence intervals for the proportions of habitat use (o_{i+})		Habitat availability (KDE95%) Π_i	Selection	Bonferroni's confidence intervals for the average selection ratio ($\hat{w}_i$)	
			Lower	Upper			Lower	Upper
Elama	Riffle	2176	0.615	0.659	0.502	Positive	1.265	1.347
	Run	1130	0.310	0.352	0.466	Negative	0.642	0.729
	Pool	110	0.024	0.040	0.033	Null	0.864	1.308
Leitzaran	Riffle	2289	0.818	0.856	0.490	Positive	1.626	1.719
	Run	406	0.130	0.166	0.441	Negative	0.293	0.396
	Pool	40	0.009	0.021	0.068	Negative	0.046	0.384

'Habitat use' shows the successive active position recordings – location points or fixes – taken with time lapses of 5 min or greater. 'Habitat availability' shows the proportion of each habitat type in each stream (kernel 95%).

FIGURE 6 Habitat selection diagrams in the Elama (a) and Leitzaran (b) streams. Circles mark the combination of habitats available for each animal (taking into account the proportion of available habitat between 0 and 1 for each microhabitat), whereas the arrows point to the habitat combination used (taking into account the proportions of habitat used between 0 and 1 for each microhabitat). Pink dots mark the mean habitat availability and green dots mark the mean habitat use in each stream section
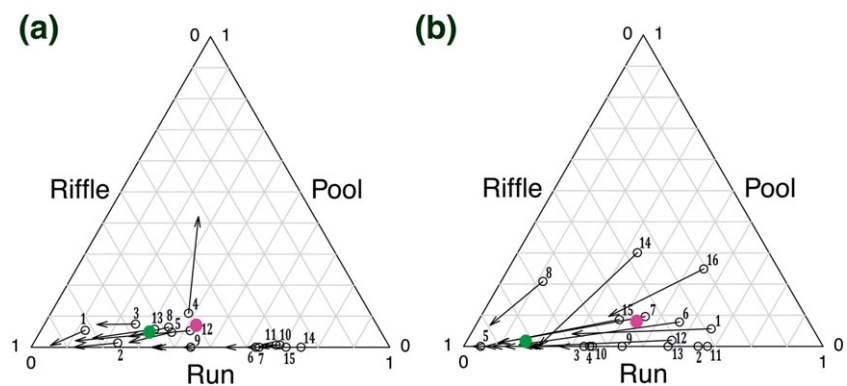
shelters. Their results might be strongly biased, however, because these reaches are precisely the type where desman faeces are more detectable. In reaches without emerging structures desmans tend to deposit their faeces in bank refugia, where they are hardly detectable, resulting in false absences (Charbonnel et al., 2015; González-Esteban et al., 2003b; Nores et al., 1999). These research studies can only indicate the type of streams where desman faeces are more easily detectable, and do not show how desmans use the space in the streams that they inhabit. The study presented here partly fills this gap, showing a consistent need for speed, i.e. a strong preference for riffles and a clear avoidance of pool habitat, thus confirming the first hypothesis. Only

one individual showed a preference for pools. After close inspection of the home range of this individual, we could find no clear explanation for its behaviour. It might have resulted from some patches of high prey availability, but, given the precision of the locations, this hypothesis could not be tested without engaging in highly destructive benthos sampling.

Apart from this one individual, the rest showed preference for swift microhabitats, probably related to food, shelter, or hydraulics. Regarding food, riffles have been reported to harbour higher invertebrate diversity and biomass than stream habitats with slower water velocities (Dewson et al., 2007; Hussain & Pandit, 2012). They also

seem to harbour higher secondary production (Buffagni & Comin, 2000; Polis, Anderson, & Holt, 1997), although the trend is far from universal (Wohl, Wallace, & Meyer, 1995). Alternatively, riffles may offer better shelter than either runs or pools because typically they have more emerging boulders, among which the desman can hide when eating the prey captured under water (Niethammer, 1970), or perhaps the boulders provide protection for desmans against rapid increases in flow (either natural or artificial). In addition, the fast water current in riffles may make it easier for desmans to overcome their natural buoyancy, as they often crawl on the bottom, using their strong claws to take hold (Richard, 1986).

The second hypothesis was also confirmed, as desmans used the habitat differently depending on the environmental conditions of the stream. Although animals can be expected to be less selective in lower quality areas, where they are forced to use suboptimal habitat in order to survive (Goiti, Aihartza, Garin, & Zabala, 2003; but see Garshelis, 2000, or Railsback, Stauffer, & Harvey, 2003), the opposite was observed. The pattern found for the desman may result from the least preferred habitats being worse in the Leitzaran, the stream affected by water diversions for hydropower, or reflect a decrease in selectivity in the Elama, as a consequence of a higher population density. In fact, the difficulty in capturing the same number of animals in the Leitzaran suggests a lower density of the population there. It is worth noting that foraging ranges were longer in the Leitzaran than in the Elama, which emphasizes either poorer habitat suitability or larger population pressure in the Leitzaran. Moreover, the smaller foraging ranges observed in the Elama suggest that the use of pools in this river was not a consequence of a higher population pressure and intraspecific competition. Thus, the overall results indicate that the less preferred habitats in the Elama were not as unsuitable as in the Leitzaran, either in prey availability or in physical characteristics (e.g. shallower depth, slower flow).

Whatever the reason, the results show that the Pyrenean desman positively selects riffles rather than runs or pools, and more so in rivers affected by water diversion. Water diversion reduces the wetted channel (Stanley, Fisher, & Grimm, 1997), alters hydraulics (McIntosh et al., 2002), reduces the populations of benthic invertebrates (James, Dewson, & Death, 2008), and exerts impacts on stream ecosystem functioning (Arroita et al., 2017). The results suggest that water diversion can also have detrimental effects on the habitat of the endangered Pyrenean desman by reducing the availability of its preferred microhabitat. Aymerich (2004) proposed that the artificial reduction of flow regime (e.g. as a result of hydropower production or irrigation) is likely to have an adverse impact on the Pyrenean desman, especially in mountain rivers that are more sensitive to flow reduction. In addition, desmans are observed at times in the diversion canals of hydropower schemes (MAGRAMA, 2013), probably when animals travelling downstream in search of new territories follow the canal instead of the water-scarce stream channel. It is unclear what happens to these animals, but dying in the turbines is not an unlikely outcome (Elosegi, 2010). Reduced flows in general, and water diversion in particular, are also known to have detrimental effects on other stream species, including salmonids (Bradford & Heinonen, 2008; Heggenes, Saltveit, & Lingaas, 1996) and the dipper (Chen & Wang, 2010), a genus of birds that also favours riffles (Logie, Bryant, Howell, &

Vickery, 1996) and apparently exploits a trophic niche similar to that of desmans (Santamarina, 1993).

As for the management implications of the present findings, we suggest that environmental flow allocations should be revisited in streams with desman, especially in those such as the Leitzaran Stream that are designated as Special Areas of Conservation (SACs) within the Natura 2000 network. Instead of relying on the simple hydrological formulae used at present, specific hydraulic studies should be undertaken to determine how discharge affects the abundance and distribution of riffles in each bypassed section, and to discern whether there is any tipping point that should not be crossed, i.e. a threshold of discharge diverted beyond which habitat availability falls rapidly. Arroita et al. (2017), using experimental flow manipulation in a stream similar to the Elama, demonstrated that environmental flows, as currently defined in the Basque Country, still severely reduce flow velocity and riffle abundance, thus strongly affecting stream ecosystem functioning. Therefore, it is likely that the very abundant diversion schemes in headwater streams in the Basque Country (Ente Vasco de la Energía (EVE), 1995), and elsewhere, are severely affecting desman habitat quality.

In addition to environmental flows, management actions that reduce riffle availability should be avoided. In the province of Gipuzkoa alone, where the Leitzaran Stream is, there are more than 900 low dams and weirs in a territory of less than 2000 km^2 (BOE, 2016; EVE, 1995). Most of these structures are legacies of past activities such as mills or iron foundries, and collectively create large areas of stagnant water, probably of little use for desmans as pools. These weirs should be taken down where possible, preserving only those currently in use or with heritage value. Channelization has also been described as detrimental to desman habitats (MAGRAMA, 2013), although with little empirical evidence. The present results suggest that channelization can be especially detrimental when it reduces flow velocity and heterogeneity, which is common in engineered channels with trapezoidal cross sections designed to increase flood conveyance capacity. Among restoration activities that might improve desman habitat is the introduction of large wood in the river, especially forming deflectors to create riffle-like areas, as has often been used to improve salmonid habitat (Nagayama & Nakamura, 2010).

The present research points to the availability of fast-flowing riffle areas as a key factor in habitat quality for the Pyrenean desman, thus highlighting specific management activities that could improve the conservation status of this speed-needing species. Given the highly fragmented characteristics of the desman population, these actions should, most likely, be combined with others, such as genetic studies and individual relocation, if the endangered status of this species is to be improved.

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ORCID

Amaiur Esnaola http://orcid.org/0000-0001-5030-385X
Jorge González-Esteban http://orcid.org/0000-0002-8867-0740
Arturo Elosegi http://orcid.org/0000-0001-8809-8484
Aitor Arrizabalaga-Escudero http://orcid.org/0000-0002-6294-8492
Joxerra Aihartza http://orcid.org/0000-0003-0882-8964

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