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Geographical and sexual differences in body size of common genets, *Genetta genetta* (Viverridae, Carnivora), in south-western Europe (Iberian Peninsula)

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Abstract. Animals' body size varies intra-specifically and geographically among populations, and many species (including small carnivores) show sexual dimorphism and larger individuals (lower superficial area/volume ratio) inhabiting cooler climates complying with Bergman's rule. In the present study we analyse data of common genets wild-caught in three different regions of the Iberian Peninsula, searching for variations in size and weight between males and females, testing for sexual dimorphism, as well as for micro-scale geographical variations among populations in biometrics and sexual dimorphism. We use field measurements such as length (body and tail) and weight, to characterise the three populations in the Iberian Peninsula. Our results show that Iberian genets present significant differences between sexes, although sexual dimorphism is lower than in other small carnivores, and that they comply with Rensch's rule, males size showing greater variation. Iberian genets also follow the Bergman's rule, being bigger and heavier in colder and northern regions. Although we have detected morphometric differences among studied populations, sexual dimorphism indexes varied little. We discuss our results in the light of the different hypotheses given to explain the sexual dimorphism in carnivores, trying to identify the mechanisms that might play a role in the dimorphism of genets.

Key words: Bergman's rule, biometrics, geographical variation, Rensch's rule, sexual dimorphism

Introduction

Body size drives individual metabolic rates and energy requirements, thus being a limiting factor to the ecology of a population. It affects and is affected by the available resources and the needs of their defence, the probability of being preyed upon, the size of potential prey, their movement ability (daily, migration and dispersal), physiological efficiency, developmental times and mortality rates (Meiri 2004). Furthermore, abiotic factors such as climate

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and geographical location have also been suggested as one of the major drivers of carnivores' body shapes and sizes (Gittleman 1985). However, climate also affects directly or indirectly the biotic factors listed above (e.g. prey type and availability, physiology, etc.). The body size of small carnivores often comply with Bergman's rule, with animals being larger in cooler climates compared to those in warmer regions, body mass being the most consistent character with the rule (Meiri & Dayan 2003, Diniz-Filho et al. 2007). However, this broad pattern has been shown to vary between biogeographical eco-regions (e.g. confirmation of mammalian Bergmans' trends in cold macroclimates but not in the southern Neotropics; Rodríguez et al. 2008) or even between related species (e.g., *Vulpes vulpes* and *Vulpes velox*, Meiri & Dayan 2003). The study of an animal's size and its geographical variation is, therefore, fundamental to understand if there are regional adaptive solutions, as well as to recognize each species role in a given community.

Intra-specific body variation and specifically inter-gender discrepancies have evolutionary relevance and can be the result of separate selective pressures or of a strategy to avoid intra-specific competition by enabling the sexes to exploit different food resources (Moors 1980). This is particularly true in males, whose body size varies more than that of females in related species or populations, resulting in an increasing or decreasing sexual dimorphism, in male or female size biased species respectively, which is known as Rensch's rule (Blanckenhorn et al. 2006).

The common genet (*Genetta genetta* Linnaeus, 1758) is a small carnivore belonging to the viverrid family, being native to Africa (Lariviére & Calzada 2001). European populations of the common genet are genetically related to the Magrebian genets (western North Africa), which were likely introduced throughout the Mediterranean Basin 1000–1500 years ago from North Africa by Algerians as a domestic animal, afterwards spreading through south-western Europe (Lariviére & Calzada 2001, Gaubert et al. 2009). Nowadays, the species is common on the Iberian Peninsula (Spain and Portugal), the Balearic Islands and the southwestern part of France, with some sporadic observations in northern countries (Livet & Roeder 1987). Despite its abundance (reaching 0.70 genets/km^2; Sarmento et al. 2010), the common genet still remains one of the lesser known carnivores inhabiting Europe and only in the last decade has the species become the focus of several ecological studies, but none addressing the implications of sexual dimorphism in the adaptation context (e.g. Saint-Girons 1973, Delibes 1974, Calzada 1998, Aihartza et al. 1999, Lariviére & Calzada 2001, Costa & Santos-Reis 2002, Zuberogoitia et al. 2002, Rosalino & Santos-Reis 2002, Santos-Reis et al. 2004, Rosalino et al. 2005, Espírito-Santo et al. 2007, Zabala et al. 2009). The species has nocturnal habits (Santos-Reis et al. 2004), is territorial (home ranges ranging, on average, from 3.46 to 5.2 km^2; Zuberogoitia et al. 2002, Santos-Reis et al. 2004) and may travel 50 km during its dispersal (although the mean distance between resting sites may reach 0.73 km, Larivière & Calzada 2001).

The goals of the present study are two-fold: to understand whether Iberian genets present sexual dimorphism and if so, if it varies with geographical location. More specifically we want to determine: (1) if there are variations in size and weight between males and females; and (2) if there is geographical variation in the sexual dimorphism within the Iberian Peninsula. We expect that genets, as other small carnivores exhibiting sexual dimorphism, will follow Rensch's rule with male body size being more variable than that of females. We also expect that genets of both sexes will comply with Bergman's rule, with a stronger effect of latitude on males given their larger body size variation.

Study Area

The study was conducted with data from three different areas of the Iberian Peninsula (SW Europe, Fig. 1): Biscay, Basque Country (Spain); Collserola Park, Catalonia (Spain); and Serra de Grândola, Baixo Alentejo (Portugal).

Biscay (43º 21' 00" N)

The study area covers 2236 km² with a population about 1.2 million inhabitants. The landscape is hilly and rugged, and altitude ranges from 0 to 1475 m a.s.l. The climate is oceanic, with annual rainfall ranging between 1200 and 2200 mm, average winter temperature of 8.7ºC and of 17.6ºC in summer. Winters are mild and there is no summer drought. In the mountains and valleys, apart from urban areas, land is mainly devoted to forest plantations of *Pinus radiata* and *Eucalyptus globulus* that occupy more than half of the surface of Biscay. Traditional hamlets with small orchards and fruit gardens are frequent and widespread. Meadows, and pastures grazed by dairy cattle and sheep are not uncommon, but tend to be concentrated in the western part of the study area. Most agricultural activities concentrate in small parcels interspersed in a mosaic of different land uses, with extensive arable lands being absent.

Collserola (41º 26' 16" N)

Collserola Park is a periurban park adjacent to the large conurbation of Barcelona city, situated 7 km from the coast in northeastern Spain. This is an area of around 8000 ha, with almost 3 million inhabitants, and a high number of visitors in woodland habitats throughout the year. Altitude varies from 60 to 516 m a.s.l. The climate is typically Mediterranean, with moderate temperatures and scarce rainfall (ranging between 595 and 640 mm), which is concentrated in the autumn and spring. The average summer temperature is 23.2ºC, and 10.8ºC in winter. In general, the summers are hot and dry, and the winters are not particularly cold or humid (Camps & Llimona 2004). This area is dominated by *Pinus halepensis* woodlands mixed with *Quercus ilex* and *Q. cerrioides*. There are well developed understorey patches, composed of species such as *Erica arborea*, *Viburnum tinus*, *Arbutus unedo* and *Rhamnus alaternus*. Vegetation is denser along valley bottoms, with an abundance of *Hedera helix*, *Clematis vitalba* and *Smilax aspera*. The remaining area is made up of Mediterranean anthropogenic environments, which form a complex mosaic of fields, scrubland, maquis vegetation, crops, abandoned crops and suburban areas.

Grândola (38º 10' 00" N)

The Portuguese study area is located in Serra de Grândola, a moderately rolling coastal mountain, with elevations varying from 150 to 270 m a.s.l., located in the southwest, 115 km south of Lisbon. The area encompasses 1100 ha, and has a low human density (18.5 ind/km^2), with people concentrated in few small villages and in the city of Grândola (Loureiro 2008). This region is characterized by a Mediterranean climate with Atlantic influences (humidity), showing a clear seasonal variation in temperature and precipitation. The average winter temperature is 11.2ºC, the average summer temperature 22.2ºC, and the annual precipitation ranges between 137 and 500 mm (Correia & Santos-Reis 1999). Winters are temperate, with some precipitation, and summers are hot and dry (Loureiro 2008). Serra de Grândola encompasses one of the most homogeneous and extensive stands of *Quercus suber* (with and without understorey) in Portugal (Costa & Pereira 2007), functioning as a matrix where other landscapes units are interspersed: riparian vegetation, orchards and *Olea europaea* yards, pastures, scrubland and *Eucalyptus globulus* stands (Rosalino 2004). The human activity in that area includes mainly cork extraction, although extensive cattle breeding together with Iberian black pigs, sheep and goats as well as honey, mushroom and wood production are also important (Rosalino 2004).

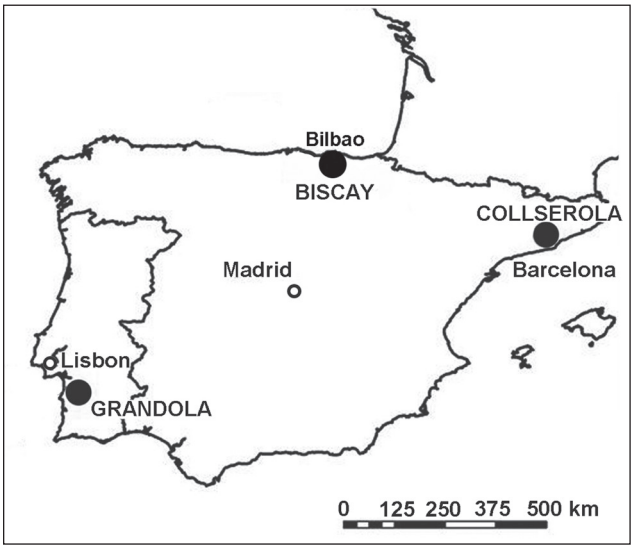

Fig. 1. *Location of study areas.*

Material and Methods

Trapping

A) Biscay: Live-trapping was conducted in five different surveys: two extensive trapping campaigns (October 2004 to January 2005 with a total effort of 1259 trap-nights (TN) and from October 2007 to January 2008 with a total effort of 2242 TN), and three trapping seasons restricted to concise areas in Natural Parks occurring from 1998 to 2003 with an effort of 4049 TN. Fifty-five genets were captured (34 cubs/juveniles and 21 adults).

B) Collserola: Genets were captured between June 1999 and June 2001, with a total effort of 216 TN. Seventeen genets were captured (2 cubs/juveniles and 15 adults).

C) Grândola: From 1997 to 2002, genets were captured yearly between February and August, corresponding to a total of 4653 TN. Forty-one genets were captured in Grândola (10 cubs/juveniles and 31 adults).

Once captured, genets were immobilised and anaesthetised. Body mass and main length dimensions of the animal were recorded (see *Biometrics*). Gender was determined by checking genitals, and age was determined using three age ranges according to the teeth condition (milk teeth = cubs, definitive new teeth = juveniles, different degree of waste in teeth = adults).

Biometrics

Head and body length (BL, cm), tail length (TL, cm), and weight (W, g) were recorded to characterise the size of the different genet populations.

To quantify the sexual size dimorphism, we used the index proposed by Lovich & Gibbons's (1992), for each population and for all combined. This Sexual Dimorphism Index (SDI) is calculated as a ratio between the average size of the larger sex and that of the smaller sex adding one to situations where males are larger than females [SDI = (mean size of larger sex/mean size of smaller sex) +1].

To test if the body size varied across populations, we calculated two values analogously to SDI following Blanckenhorn et al. (2006): to test for Rensch's rule, we used the reduced major axis (RMA) slope which can be estimated using the ratio of male to female standard deviations, i.e., RMA = [(SD of larger sex/ SD of smaller sex)/(size of larger sex/size of smaller sex)] -1; and to test for Bergman's rule we calculated the Bergman clines using the corrected slope ratio (CRS), that is sex-specific latitudinal slopes, i.e. CRS = [(slope of the larger sex/slope of smaller sex) / (size of the larger sex/size of smaller sex)] -1. Both values correct the scaling effect with sexual dimorphism neutralizing it in a manner equivalent to log-transforming the original data (Blanckenhorn et al. 2006). According to those authors the Rensch's rule holds when RMA (which is scaled for the degree of dimorphism) is greater than zero.

Statistics

Normality and homogeneity of variance were tested using the Kolmogorov-Smirnov and Levene's test (Krebs 1989). Body length for the Grândola population did not fulfil the latter, and therefore was log-transformed (Log10). Inter-gender differences in biometrical variables (body length, tail length and weight) at population level were tested with a Student's t-test. To avoid bias due to differences in developmental stages at capture (Thom et al. 2004), cubs and juveniles were not included in the analyses. To test for differences between the proportion of each sex among the three populations, a contingency table with a chi-square test was used (Zuur et al. 2007). A multivariate analysis of variance (MANOVA) was used to evaluate differences in body size and weight of Iberian genets among sexes and geographical areas.

Results

The proportions of males and females in the three studied populations were not significantly different (χ^2 = 0.570, df = 2, p = 0.752) and therefore the influence of sample size was considered negligible, allowing us to pool the data for further analysis.

For the three body measurements taken, males were bigger than females (Table 1), yielding a positive SDI (Table 2, Fig. 2a–c). These Iberian populations follow Rensch's rule, with male size being more variable

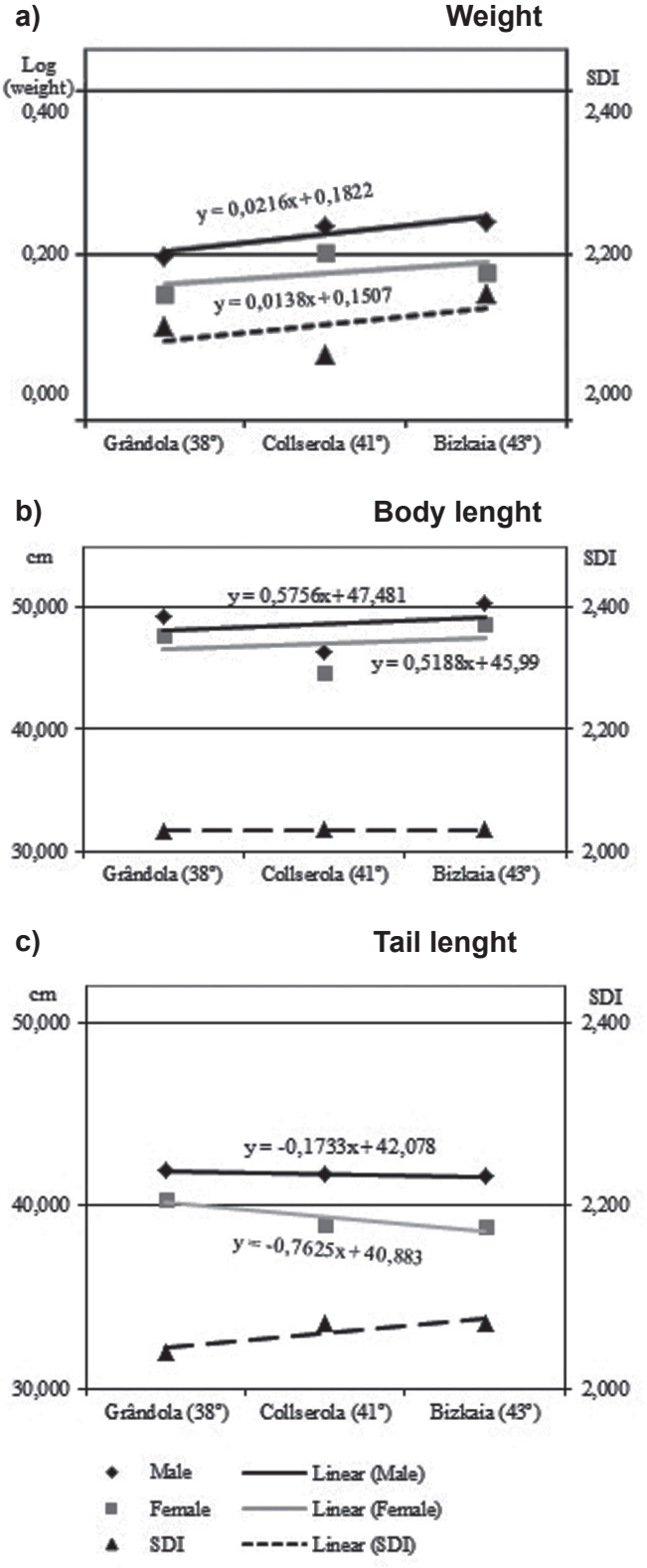

Fig. 2. *Bergman's slopes for weight (a), body (b) and tail length (c), and their Sexual Dimorphism Index (SDI) among the studied genet populations.*

Table 1. *Basic statistics and statistical tests of the body size variables for the three genet populations and the total of Iberian genets. (BL = head and body length; TL = tail length; W = weight).*

	BL (cm)	TL (cm)	W (g)
Males			
Biscay (n = 11)	50.7 ± 2.8	41.5 ± 1.2	1745 ± 156
Collserola (n = 6)	47.1 ± 1.2	42.7 ± 2.3	1908 ± 150
Grândola (n = 15)	49.2 ± 3.5	41.9 ± 2.0	1580 ± 234
TOTAL (n = 32)	49.3 ± 3.2	41.9 ± 1.8	1698 ± 229
Females			
Biscay (n = 10)	48.4 ± 3.0	39.9 ± 1.7	1529 ± 158
Collserola (n = 9)	45.2 ± 1.4	38.9 ± 3.3	1633 ± 164
Grândola (n = 16)	47.7 ± 2.1	40.3 ± 1.6	1420 ± 185
TOTAL (n = 35)	47.3 ± 2.5	39.6 ± 2.2	1506 ± 190
Males – females			
Biscay	t = 1.763	t = 3.988**	t = 3.135*
Collserola	t = 2.657*	t = 2.384*	t = 3.278**
Grândola	t = 1.418	t = 2.462*	t = 2.112*
TOTAL	t = 2.941*	t = 4.699***	t = 3.749**

than female size, yielding a RMA greater than zero for all measurements (Table 3). Moreover, male Bergman clines are steeper than those of females (Table 3), confirming this higher variability in males.

When testing sexual dimorphism for all populations combined, all measurements are statistically dimorphic (Table 1). However, only tail length and weight were significantly dimorphic variables in the three studied populations when tested separately (Table 1). Weight was the most dimorphic feature (Table 2) with males being 11 to 17% heavier than females depending on the study area.

We found significant differences among populations in body length and weight (Table 4), and the same applies when considering the three populations together while comparing the gender; however, no population effect was detected in the sexual dimorphism (Table 4).

Table 2. *Sexual dimorphism index (SDI) in the three genet populations. (BL = head and body length; TL = tail length; W = weight).*

	BL	TL	W
Biscay	2.047	2.040	2.141
Collserola	2.042	2.098	2.267
Grândola	2.031	2.040	2.113
TOTAL	2.043	2.060	2.127

Table 3. *Body size parameters for Iberian Genets (following Blanckenhorn et al. 2006): Reduced major axis (RMA) and corrected slope ratio (CRS). (BL = head and body length; TL = tail length; W = weight).*

	RMA	CRS
BL	1.961	2.073
TL	1.195	1.214
W	1.918	2.595

Table 4. *Effect of location and gender in the size and weight of common genets tested by Multivariate Analysis of Variance (MANOVA). (BL = head and body length; TL = tail length; W = weight).*

	BL		TL		W	
	F	P	F	P	F	P
Location	6.787	0.002	1.843	0.167	12.313	< 0.001
Sex	5.492	0.022	2.963	0.090	22.741	< 0.001
Location*sex	0.022	0.978	1.056	0.354	0.647	0.527

Discussion

Size variation and sexual dimorphism in carnivores has been explained with hypotheses based on biogeography and sexual selection (Ralls & Harvey 1985, Meiri & Dayan 2003, Diniz-Filho et al. 2007). Iberian genets seem to follow Bergman's and Rensch's rules, but as our results are based in only three populations, they should only be seen as indicative

of the geographical variations. Genets body weight and length show a positive slope with increasing latitude (tail length did not differ among locations), showing greater variation in male size, indicating that both rules may be related at the species level (Blanckenhorn et al. 2006). Although it is usually accepted that Rensch's rule can be applied to inter-specific variation in sexual size dimorphism but not to intra-specific or among population variation, some exceptions were already detected (e.g. Young 2005). These exceptions are usually related with a stronger directional sexual selection on male body size than fecundity selection on female body size or with constrains of environmental factors (Blanckenhorn et al. 2006).

Interestingly, we found that sexual dimorphism indexes are maintained without variability (no statistical differences) in the three studied populations, independent of the morphometric differences detected among them. Whereas the body structure of genets in the Iberian Peninsula has adapted to local environmental conditions and available energy (Webster et al. 2004), the mechanisms involved in maintaining the sexual dimorphism seem to have remained invariable even considering populations separated more than 500 km among them. This adaptation to different local environmental conditions is remarkable if we consider that most likely common genets have only recently been introduced into Europe and descend from a reduced number of individuals (Gaubert et al. 2009). There are significant correlations between body size and the environment which support the idea that Darwinian adaptation can explain body size evolution expressed both as an effect of niche conservatism (phylogenetically structured environmental variation) and as unique and independent adaptive responses of each species/populations to environmental conditions (Webster et al. 2004, Diniz-Filho et al. 2007). Climate affects animals' body length and weight, which increase towards northern and colder climate areas. Rodríguez et al. (2006) suggested that in lower latitude areas, topography, which influences habitat complexity and species distribution and abundance may have a greater role in constraining body sizes. As regards Iberian genets, we believe that both mechanisms might be constraining their body size: temperature would induce greater sizes (as defined by the Bergmans' rule), but since we are dealing with southern European populations, we think that prey availability (especially rodents, the main prey of genets; Rosalino & Santos-Reis 2002, Carvalho & Gomes 2004, Barrientos &Virgós 2006) which is positively correlated with body size (Yom-Tov & Yom-Tov 2004), may be also influencing our results. Moreover, the fact that several independent introductions events occurred in Iberia in different locations throughout the Mediterranean Basin (Gaubert et al. 2009), with the consequent dispersion, might also have contributed to the registered different genets body sizes throughout Iberia.

As regards inter-gender differences, most small carnivores present an evident sexual dimorphism, males being bigger than females (Moors 1980, Dayan et al. 1989, Lynch & O'Sullivan 1993, Dayan & Simberloff 1994, Holmes & Powell 1994, De Marinis 1995, Lynch & Hayden 1995, Macdonald 2002, Thom et al. 2004, Wisely et al. 2005). Genets are no exception and previous studies (e.g. Saint-Girons 1973, Delibes 1974, Calzada 1998, Lariviére & Calzada 2001, Rosalino et al. 2005), as well as our results, have demonstrated that they follow this pattern, although dimorphism seems to be lower than that observed in other species of small carnivores, namely mustelids (Dayan et al. 1989, Dayan & Simberloff 1994, De Marinis 1995, Thom et al. 2004, Wisely et al. 2005). Several theories have been put forward to explain sexual dimorphism. On the one hand, it may be driven by competition between males for the access to females, leading into different spatial distribution and home range sizes between sexes (Lynch & O'Sullivan 1993). However, the spacing behaviour of genets follows a contrasting pattern in the Iberian Peninsula: in the North, male genets have significantly larger home range than females (Zuberogoitia et al. 2002, Camps & Llimona 2004, Zuberogoitia & Zabala 2004) whereas in the South, male and female home range sizes are similar (Palomares & Delibes 1994, Santos-Reis et al. 2004). Indeed, research on small carnivores shows that sexually dimorphic species have different micro-habitat preferences (Zabala et al. 2007a, b). This last issue remains unstudied in most small carnivores, but it could be an important factor for home range sharing between conspecifics of opposite sexes. On the other hand, it has been proposed that males are expected to be larger than females as a means to reducing intra-specific competition for food (Dayan et al. 1989, Dayan & Simberloff 1994, Thom et al. 2004). The diet of genets in Iberia is based on the consumption of fruit, small mammals, birds, arthropods, amphibians and reptiles (Virgós et al. 1999, Rosalino & Santos-Reis 2002, Carvalho & Gomes 2004, Barrientos & Virgós 2006, Santos et al. 2007) but there are no sex-specific investigations. Zalewski (2007) however

proved that contrarily to that expectation, despite male pine martens (*Martes martes*) being heavier than females they did not consistently consume larger prey than females. The dimorphism in prey size in male and female diets and food niche partitioning depended on rodent abundance and geographical locations. Zalewski (2007) suggested that neither prey composition nor prey size alone explain the direction of size dimorphism in the pine marten. Bolnick & Doebeli (2003) stated that although resource partitioning between sexes has been observed in carnivores, such dimorphism may be the result of sexual selection instead of ecological character displacement. For instance, sexual selection on body size could lead indirectly to resource partitioning, because the relatively larger sex can consume larger prey. Therefore, sexual dimorphism is more likely to be caused by different selective forces acting on the sexes separately or by a combination of factors like behaviour, habitat use and morphological constraints (Zalewski 2007). Sexual selection and ecological interactions are not mutually exclusive and might interact synergistically during the evolution of sexual dimorphism (Bolnick & Doebeli 2003). As regards Iberian genets, the fact that the degree of sexual dimorphism is smaller than in other small carnivores suggests that the importance of factors driving it is not as acute as in the others. Notwithstanding, the fact that it is constant among populations shows that the causes are present and acting throughout the south-western European range with strength enough to maintain it. Further research is therefore needed to fully understand these causes.

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