Ecological interactions and species coexistence in Iberian mesocarnivore communities - Extended summary and main results

Pedro Monterroso[1,2,3]*, Paulo C. Alves[1,2,4] & Pablo Ferreras[3]

1. CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Rua Padre Armando Quintas, nº 7, 4485-661Vairão, Portugal.
2. Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4169-007 Porto, Portugal.
3. Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM), Ronda de Toledo 13, 13071 Ciudad Real, Spain.
4. College of Forestry and Conservation, University of Montana, Missoula, MT, USA.

* Corresponding author: pmonterroso@cibio.up.pt

This article is a comprehensive summary of the PhD presented by Pedro Monterroso at the University of Oporto, Portugal, on december 17th, 2013, under the supervision of Dr. Paulo C. Alves and Dr. Pablo Ferreras. The thesis was awarded by the Spanish Society of Mammalogist (SECEM) in 2014, as the best thesis about iberian mammals.

Introduction

Predators are fundamental elements of natural ecosystems (Kruuk 2002, Estes *et al.* 2011, Ritchie *et al.* 2012). They assume a crucial role as ecosystem engineers (Ritchie *et al.* 2012) affecting a variety of ecosystem functions, namely by i) enforcing top-down regulation (Prugh *et al.* 2009, Ritchie & Johnson 2009, Estes *et al.* 2011), ii) promoting ecosystem resilience against introduced species (Salo *et al.* 2008, Carlsson *et al.* 2009), iii) reducing the impact of wildlife diseases (Roemer *et al.* 2009) and iv) helping seed dispersal (Rosalino & Santos-Reis 2009). One of their most promoted functions is the enforcement of top-down regulation, which has cascading effects over the entire ecosystem (Ripple & Beschta 2006, Ripple & Beschta 2008, Prugh *et al.* 2009, Ripple *et al.* 2010, Levi & Wilmers 2012). This top-down control acts on two levels: demographic (density-mediated effects), by constraining the population numbers of prey and subordinate competitors (e.g. Ripple & Beschta 2012); and behavioural, by restraining the spatial and temporal activity patterns of these groups (e.g. Laundré *et al.* 2001, Cozzi *et al.* 2012). Consequently, the composition and structure of carnivore communities is strongly influenced by interspecific competitive interactions (Donadio & Buskirk 2006, Ritchie & Johnson 2009). Intraguild predation (IGP) constitutes an intense form of interference competition (Ritchie

& Johnson 2009), and is a widespread biological interaction, especially in carnivore communities (Palomares & Caro 1999, Arim & Marquet 2004). Its intensity is mediated by relative body size, feeding ecology, prey availability and predatory habits of the species involved (Palomares & Caro 1999, Donadio & Buskirk 2006). However, direct lethal encounters are probably just a small part of all competitive interactions among coexisting carnivores (Ritchie & Johnson 2009). The "ecology of fear" (Brown *et al.* 1999) and its spatially explicit representation - the landscape of fear (Laundré *et al.* 2001) - are also applicable in the framework of intraguild competitive interactions (Scheinin *et al.* 2006). Dominant competitors (apex predators) can influence the distribution and behaviour of subordinate competitors (mesocarnivores) through the fear of IGP (Roemer *et al.* 2009). Therefore, behavioural adjustments in foraging strategies may also play a critical role in reducing agonistic encounters, promoting coexistence and biodiversity (Linnell & Strand 2000). Examples of such behavioural-mediated effects have been reported in several systems across the world as a means to promote coexistence between sympatric competitors (Ritchie *et al.* 2012). The effects most frequently reported are the limitation of accessibility to the most favourable habitats (Palomares *et al.* 1996, Mitchell & Banks 2005, Harrington & Macdonald 2008) and/or to the most profitable prey (Moreno *et al.* 2006, Cupples *et al.* 2011), and

temporal segregation (Di Bitetti *et al.* 2009; Cozzi *et al.* 2012; Gerber *et al.* 2012). Schoener (1974) argued that in competitive systems, increased community complexity would force coexisting species to segregate over more niche dimensions to preserve minimal resource overlap. The most important niche dimensions over which competing species segregate have been identified, in order of importance, as: habitat (spatial), food-type (trophic) and temporal dimensions. Reports of the spatial interactions among sympatric mammalian carnivores have been a particularly common focus in the attempt to evaluate competitive relations. Described patterns of spatially explicit responses among competitors include complete exclusion (Rosellini *et al.* 2008, Balestrieri *et al.* 2010), changes in habitat selection at the landscape scale (Fedriani *et al.* 1999, Fedriani *et al.* 2000, Fisher *et al.* 2013), and behaviourally mediated spatial avoidance (Harmsen *et al.* 2009, Broekhuis *et al.* 2013). Regardless the potential diversity of spatial responses exhibited by sympatric competing mammalian carnivores, the spatial niche dimension remains as one of the most important mediating competitive interactions because it entangles accessibility not only to adequate habitats, but also to prey (Fedriani *et al.* 2000, Ritchie & Johnson 2009, Wilson *et al.* 2010). Time is another niche dimension over which interacting animals might segregate to reduce the effect of agonistic encounters (Carothers & Jaksić 1984, Kronfeld-Schor & Dayan 2003). The presence of competitors frequently influences activity patterns through interference competition, which is expected to be stronger whenever similarity in other niche dimensions and body mass are high (Schoener 1974, Linnell & Strand 2000, Donadio & Buskirk 2006, Ritchie & Johnson 2009). However, the activity pattern exhibited by a mammalian carnivore is context-dependent, as it is determined by its endogenous regulation (Kronfeld-Schor *et al.* 2001, Kronfeld-Schor & Dayan 2003) and by external abiotic and biotic factors (Kitchen *et al.* 2000, Harrington *et al.* 2009, Theuerkauf 2009, Cozzi *et al.* 2012). Hence, the interaction with these factors can change the ultimate expression of the species diel activity. Temporal partitioning has been reported among several carnivore assemblages, and it can be exhibited by a clear asynchrony in their foraging patterns (Di Bitetti *et al.* 2009, Harrington *et al.* 2009, Gerber *et al.* 2012). The intensity of the relation between carnivores' requirements and

prey availability vindicate the competitive stress among sympatric predators that share the same prey (Gittleman & Harvey 1982, Carbone *et al.* 1999), especially when prey availability is limiting (Linnell & Strand 2000, Donadio & Buskirk 2006, Ritchie & Johnson 2009). Most research on the evaluation of competition between carnivores along the trophic niche dimension, often consist of two or three-dimensional approaches by evaluating dietary and spatial (and/or temporal) patterns simultaneously (Fedriani *et al.* 2000, Mitchell & Banks 2005, Harrington *et al.* 2009, Hass 2009). The contrasting results of such approaches depict the variability of trophic relationships among coexisting mammalian carnivores, emphasizing that the complexity of such interactions can only be understood when evaluated in a multidimensional framework.

Southwestern (SW) European terrestrial carnivore communities include a total of 17 species (Cabral *et al.* 2005, Palomo *et al.* 2007). However, given the limited distributional range of apex predators in the IP, carnivore communities across a large portion of Iberia are strictly constituted by meso and small carnivores. However, they do not always occur in sympatry or coexist spatially within their distribution areas (Cabral *et al.* 2005, Palomo *et al.* 2007). As a consequence, mesocarnivore communities vary geographically in composition and structure, potentially compelling interspecific relations between the same pairs of species to between areas. Additionally, the differences in the availability of prey between the bioclimatic regions of the Iberian Peninsula should also provide interesting contrasts in the interspecific interactions among carnivores.

The challenges involved in monitoring carnivores make the use of direct and invasive methods laborious, often inefficient and potential hazardous for the animals (Long *et al.* 2008, Kelly *et al.* 2012). Also, their large spatial requirements, preferred habitats, low densities, and elusive behaviour deem carnivores difficult to study. The recent technological advances both in conservation genetics (Beja-Pereira *et al.* 2009, Shehzad *et al.* 2012) and field techniques (O'Connell *et al.* 2011), coupled with developments in statistical methods such occupancy models (Mackenzie *et al.* 2006) or modelling of daily routines (Ridout & Linkie 2009) have enhanced the value of non-invasive methods for studying terrestrial carnivores. The widespread use of these methods has promoted their common

use to monitor multiple carnivore species across large areas at a relatively modest cost (Weaver *et al.* 2005, Zielinski *et al.* 2006, Long *et al.* 2007). The molecular and technological advances are not only useful, but also required to assess the validity of these sampling methods or propose further refinements.

Taking advantage of the geographically-inherent variability of the Iberian biological systems, two main objectives were defined and addressed in two distinct sections: i) to assess the reliability and improve current sampling methods for ecological studies of mesocarnivores in Southwestern Europe; and ii) to study the strategies that allow coexistence among mesocarnivores in SW European communities.

In this extended summary, the main results are outlined and integrated to provide an overview of the addressed objectives contributing to the understanding of mesocarnivore community functioning and methodological advances in the study of such communities.

Material and methods

Study areas

Five sampling sites in the Iberian Peninsula were selected based on criteria of ecosystem integrity and representation of the existing carnivore communities. These sites represent the two main biogeographic regions of the Iberian Peninsula: the Mediterranean region, which occupies roughly 2/3 of the southwestern IP, and the Atlantic region, which is restricted to the northern fringe and extends towards the Pyrenees (European Environmental Agency 2012); and include the communities with and without apex predator presence, and varying abundances of the main prey species, the European rabbit. Within each study site, a sampling area of approximately 6,000 ha was selected. The study areas were the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP), located in Portugal, and the Cabañeros National Park (CNP), the Sierra de Andújar Natural Park (SANP), and the Muniellos Natural Reserve (MNR), located in Spain. GVNP, CNP, and SANP are included in the Mediterranean region (Rivas-Martínez *et al.* 2004), where scrublands are mainly associated with steeper slopes, elevation ridges, and main water bodies. At CNP and GVNP, areas with

gentler slopes are mainly occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*) scattered within a grassland matrix (García-Canseco 1997), whereas at the SANP, such areas are rather dominated by Stone pine (*Pinus pinea*) and Maritime pine (*Pinus pinaster*) forests with and without understorey (Gil-Sánchez *et al.* 2006).

Human access is highly restricted to the selected study areas in CNP and SANP, while in GVNP about 86 % of the land is included in hunting estates. The PGNP and MNR are included in the Atlantic region (Rivas-Martínez *et al.* 2004). The landscapes consist of mountainous agricultural-forest mosaic, where mountaintops are mostly dominated by scrublands habitats and mountain slopes and valleys are essentially dominated by oligotrophic oak forests with *Quercus* sp., *Betula* sp., and *Fagus* sp. Pastures, agricultural fields, and small villages are found mainly along valleys and lower altitude locations (Prieto & Sánchez 1996, Carvalho & Gomes 2004). High levels of visitation occur at the PGNP study area, whereas human access is limited inside the integral reserve of MNR.

Field sampling

Field sampling consisted of multi-method approach to ensure high-quality data on the distribution, abundance and activity of mammalian carnivores and their main prey. The methods selected were employed as follows: *i) camera-trapping* - camera traps were uniformly spaced in each study area following a grid sampling scheme, with a mean distance between neighboring cameras of ~1.4 km. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, MS, USA) and Scout-Guard (HCO OutDoor Products, Norcross, GA, USA). Cameras were mounted on trees approximately 0.5- 1.0 m off the ground and set to record time and date when triggered and maintained in the field for a period ≥28 days. Cameras were inspected for battery or card replacement every 7-14 d. A combination of carnivore attractants was used to incite animals' curiosity and thus increase detection probabilities; *ii) scat searching* - within each study area, 10 transects, 3 km long each, were designed along unimproved roads or trails for active searching of carnivore signs. Each transect was sampled twice per season: once at the beginning of the sampling

campaign and again after approximately 20 days. Transects were spatially distributed in order to adequately sample all existing habitats. They were surveyed on foot and all carnivore scats within a bandwidth of 2 m to each side of the transect line were collected. Scats were identified based on their location, morphology, dimensions, colour and odour, with the aid of specific field guides (Bang *et al.* 2007, Iglesias & España, 2010). Scats were collected taking all precautions to prevent contamination from the collector or cross-contamination from other samples, and preserved in plastic vials in ethanol (96%) until DNA extraction*; iii) pellet counts* - European rabbits' relative abundance was estimated using pellet counts. Fourteen to 15 grids were sampled in each study area. Each sampling grid consisted of 9-12 sampling plots, regularly spaced at 15-m intervals. Each sampling plot consisted of a circular 0.5 m² area, which was cleared of all rabbit pellets at the beginning of each sampling campaign. Sampling plots were then recounted after ~20 days post-clearing. Rabbit relative abundance was assessed as an uncorrected daily pellet accumulation rate (UNC), which was obtained by calculating the average number of pellets per square metre divided by the number of days elapsed since the initial cleaning (Fernández-de-Simón *et al.* 2011)*; iv) live trapping* - the relative abundance of murids (*Apodemus* sp. and *Mus* sp.) was assessed by the means of live captures. Using the same sampling grids and plots' placement previously described, 9-12 live traps (SFG and LFG folding traps, H.B. Sherman traps, Tallahassee, FL, USA) were set for the capture of small mammals. A trapping campaign consisted of three consecutive trapping days. All captured individuals were then identified to the species level, sexed, weighted and aged without the resort to any kind of chemical immobilization. After handling, each animal was released at the capture site.

Results

Methodological improvements for mesocarnivore ecological studies in SW Europe

The active search for carnivore signs is a non-invasive field method widely employed to study mammalian carnivores (Long *et al.* 2008). Such studies rely on the identification and analysis of scats detected in the field. However, species assignment is commonly based on scat morphology, and the potential errors in their identification are rarely accounted for and might contribute to substantial bias of the final results. Alternative methods consist in fixed stations like hair snares, track stations or camera traps (Long *et al.* 2008, O'Connell *et al.* 2011, Kelly *et al.* 2012). As abovementioned, the recent advances in molecular methods provide a means to obtain DNA from non-invasive samples from target species and communities, hence renewing the potential of hair snaring methods to fulfil the sampling requirements for carnivore monitoring. However, these methods have rarely been tested in Europe. Additionally, previous research suggests that the use of effective attractants can significantly increase detection probabilities for methods based on fixed detection stations (McDaniel *et al.* 2000, Garrote *et al.* 2012), further increasing their potential. Therefore, this work aimed to: i) assess the effectiveness of several attractants for Iberian carnivores, and to evaluate their usefulness for non-invasive survey methods; ii) evaluate the accuracy of species identification based on morphological characteristics of mammalian mesocarnivore scats collected in two areas in the Iberian Peninsula; and iii) quantitatively assess the effectiveness of hair snares for surveying mesocarnivores in the Iberian Peninsula, by comparison with camera-trapping.

To achieve the first goal, the responses of seven carnivore species to six potential attractants were evaluated through cafeteria-like experiments with captive specimens and a selectivity index was applied to assess the relative attractiveness of each tested substance. The enclosure tests were followed by field trials with camera trapping, using the most promising attractants for field evaluation of their efficiency. For the second objective, the accuracy of species identification of mammalian mesocarnivore scats collected was evaluated in the field in two study areas during two different seasons. Carnivore scats were collected following the above-described sampling protocols and were identified based on their location, morphology, dimensions, colour and odour, with the aid of specific field guides. Molecular methods were then used to provide a "true" species assignment, and the accuracy of the traditional identification procedure was modelled using generalized linear models. Finally, the third goal was pursued by evaluating the efficiency of hair snares coupled with genetic identification and camera trapping under an occupancy modelling framework (Mackenzie *et al.* 2006) to assess

method-specific detectability and occupancy estimates.

Regarding the tested attractants for mesocarnivore monitoring, the enclosure trials revealed that lynx urine was the most effective and generalist attractant because it successfully attracted six of the seven species tested. Rubbing behaviour was also induced in the greatest number of species by lynx urine. Field tests using a combination of lynx urine and valerian extract solution induced investigative behaviours in over 50% of all detection events in all species, with the exception of the Eurasian badger. Our scat identification models revealed that error rates in species assignment of scats based on morphology were highly variable, ranging from 14%, for putative red fox *Vulpes vulpes* samples, to 88%, for putative wildcats *Felis silvestris*. The developed models revealed that putative species, season, study area and target species abundance are among the factors involved in identification accuracy. However, the low variability explained suggests that unaccounted factors also had significant effects on accuracy rates.

Hair snaring sampling for mesocarnivores provided a total of 136 samples potentially belonging to mesocarnivores. Genetic identification success varied with diagnostic method: 25.2 % using mitochondrial CR, and 9.9 % using the IRBP nuclear gene. Naïve occupancy estimates were ~5.3 ±1.2 times higher with camera-trapping than with hair-snaring, and method-specific detection probabilities revealed that camera traps were ~6.7±1.1 times more effective in detecting target species. Few site-specific covariates revealed significant effects on mesocarnivore detectability.

The experiments performed in this section allowed us to conclude that no single attractant is effective for all Iberian mesocarnivore species. Nevertheless, a combination of lynx urine and valerian solution should efficiently attract the majority of species present in Iberian carnivore communities, and may be used to increase detection probabilities when coupled with remote detection methods. Furthermore, some species exhibit a rubbing behaviour when they come in contact with the attractants. Regardless of the generalist efficiency of the lynx urine, other tested substances revealed promising results for single-species monitoring. We also found that traditional expert-based identification of carnivore scats constitute a potential source of bias in ecological studies, with serious consequences for the management of threatened species, as unrealistic estimates of status and distribution are prone to occur. Our results suggest that scat identification accuracy rates are dependent on target species abundance, scat characteristics and circumstance-specific factors and therefore should not be transferred or extrapolated over time and sampling areas. Finally, we found that camera trapping is a more efficient method for detecting mesocarnivores and estimating their occurrence when compared to hair snares. To improve hair snares' low detection probabilities, the number of sampling occasions and the frequency at which hair snares are checked should be increased.

These results provide a baseline for selecting attractants and enhancing non-invasive sampling methods for the survey and monitoring programs that focus on carnivore species. The rubbing behaviours exhibited by several of the species tested suggest the use of these attractants could improve the efficiency of field studies that rely on rub-pads for the collection of biological samples. Therefore, with some refinements to increase detection rates and the success of genetic identification, hair-snaring methods may consist on a valuable cost-effective method for large scale and long term monitoring of Iberian mesocarnivores, while providing deeper insights into population parameters attained through adequate analysis of genetic information, not possible with camera traps. Finally, we advise future scat-based studies to implement measures (molecular or others) that allow researchers to determine their own circumstance-specific error rates in scat identification. Such error rates could then be incorporated in subsequent analyses, ensuring reliable ecological inferences.

Detailed information regarding the studies performed in this section can be found in the following published articles:

- Monterroso P., Alves P.C & Ferreras P. 2011. Evaluation of attractants for non-invasive studies of Iberian carnivore communities. *Wildlife Research*, 38 (5): 446-454. DOI: 10.1071/WR11060
- Monterroso P., Castro D., Silva T.L., Ferreras P., Godinho R. & Alves P.C. 2013. Factors affecting the (in)accuracy of mammalian mesocarnivore scat identification. *Journal of Zoology*, 289 (4): 243-250. doi: 10.1111/jzo.12000
- Monterroso P., Rich L.N., Serronha A.M., Ferreras P. & Alves P.C. 2014. Efficiency of hair snares and camera traps to survey mesocarnivore populations. *European Journal of Wildlife Research*. 60: 279-289. DOI: 10.1007/s10344-013-0780-1

Ecological interactions in mesocarnivore communities in the Iberian Peninsula

The structure of mesopredators' communities is complex and results from a multidimensional web of interactions such as top-down and bottom-up regulations, and intraguild interactions (Donadio & Buskirk 2006, Estes *et al.* 2011, Ritchie *et al.* 2012). However, these interactions may change geographically along species' distribution ranges as they are influenced by a diversity of factors, namely local conditions of landscape structure, prey availability and intraguild community composition (Linnell & Strand 2000, Donadio & Buskirk 2006). Therefore, the behavioural pattern exhibited by a species is expected to differ between study sites due to locally adapted interactions. Limiting similarity theory predicts that competing species must segregate along one or more dimensions of their ecological niche in order to coexist, and such segregations often occur along one of the three main ecological niche dimensions: spatial, trophic and temporal (MacArthur & Levins 1967, Schoener 1974).

In this section we aimed to: i) determine whether shifts along these dimensions can facilitate coexistence by reducing niche overlap; ii) evaluate the bidirectional relation between the diel activity strategies of these mesopredators and their mammalian prey, and iii) to evaluate the niche relations between two similar-sized mustelids with highly overlapping ecological traits - the pine marten (*Martes martes*) and stone marten (*Martes foina*) - in the southwestern limit of their range along the three main ecological niche dimensions, under a hypothesis of competitive dominance of pine martens.

The data used for temporal and spatial analyses derived from the above-described camera-trapping protocols. The analysis of selection for a period of the diel cycle and plasticity in activity patterns was evaluated using the Jacobs Selection Index (JSI; Jacobs 1974), whereas pairwise activity overlap was assessed using coefficient of activity overlap (Δ_1) and the Mardia-Watson-Wheeler (MWW) test. The strength of the interactions along the spatial dimension was modelled under an occupancy modelling framework, using single-species and two-species parameterizations (Mackenzie *et al.* 2006, Richmond *et al.* 2010). Diet analysis was performed by identifying the undigested remains present in genetically identified scats collected following the above-described sign searching protocols.

Seven species of mesocarnivores were detected and assigned to one of three behaviourally distinct groups: diurnal ($JSI_{day} \geq 0.8$), strictly nocturnal ($JSI_{night} \geq 0.8$) or facultative nocturnal species ($0.4 \geq JSI_{night} > 0.8$). Most species exhibited substantial flexibility, which allowed them to locally adapt their foraging strategies (intraspecific $\Delta_1 = 0.70\text{-}0.77$). The mean Δ_1 from all interspecific pairwise comparisons was negatively correlated with the number of carnivore species with ≥ 10 detections (r –0.76, p=0.02). Regarding the temporal relations with their prey, results revealed that even though predation risk enforced by mammalian mesocarnivores during nighttime was approximately twice and five times higher than during twilight and daytime, respectively, murids consistently displayed unimodal nocturnal behaviour. Contrastingly, despite its energetic profitability, mammalian carnivores did not exhibit a diel rhythm synchronized with European rabbits', which displayed a bimodal pattern that peaked around sunrise and sunset. We found no evidence supporting a strong spatial avoidance between stone martens or common genets and red foxes, as the models of unconditional occupancy had greater support. However, we found a basal interaction factor of ~1.30 between stone martens and common genets, suggesting that they tend to co-occur. The study performed at Peneda-Gerês National Park between pine and stone martens supported the previous results, as there was no spatial segregation between these species. Rather, coexistence was facilitated by seasonally adjusted shifts along the trophic and temporal axes in this study area. While both species often co-occurred during the season of low food resources, pine martens exploited the less profitable feeding resource (i.e. fruits). Moreover, they displayed an activity pattern that limited their access to rodents, but also reduced the probabilities of direct encounters with stone martens.

The results obtained support that the interactions between co-occurring Iberian mesocarnivores are dynamic, and their strength and direction may vary seasonally and geographically. While adjustments along the spatial dimension of the ecological niche are not a frequent strategy among co-occurring Iberian mesocarnivores, temporal segregation is likely to play an important role in facilitating coexistence, especially with increasing community complexity. Also, behavioural responses may take

place in areas of co-occurrence, where subordinate species may adopt higher elusiveness. The case study focusing on the two marten species further supports that potentially stressful interactions are preferably handled by displacements along the temporal and trophic niche dimensions, allowing sympatric intraguild competitors to spatially co-occur. Feeding resources are involved in mediating interspecific relations among potential intraguild competitors, especially when they share the same preferred prey. We suggest that the dominance position has changed in favor of the stone marten in this study area, probably as a result of habitat quality and range edge effects. Additionally, we propose that Iberian systems have probably evolved towards a situation where some degree of activity during high-risk periods benefits the overall prey population survival, while the accessibility to sufficient prey prevents predators (as a community) to completely track them. These findings also support the relative instability of interspecific interactions among similar sized species, which should be evaluated using multidimensional and site-specific approaches.These results contribute to understanding the dynamics and behavioural strategies of coexisting mesocarnivores, which are crucial for forecasting the possible outcomes of conservation or management actions.

Detailed information regarding the studies performed in this section can be found in the following published and submitted articles:

- Monterroso P., Alves P.C. & Ferreras P. 2013. Catch me if you can: diel activity patterns of mammalian prey and predators. *Ethology,* 119(12): 1044-1056. DOI: 10.1111/eth.12156
- Monterroso P., Alves P.C. & Ferreras P. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behavioral Ecology and Sociobiology.* 68 (9): 1403-1417. DOI: 10.1007/s00265-014-1748-1
- Monterroso P., Rebelo P., Alves P.C. & Ferreras P. (accepted) Niche partitioning at the edge of the range: a multidimensional analysis with sympatric martens. *Journal of Mammalogy*
- Monterroso P., Ferreras P. & Alves P.C. (*in prep*) Spatial interactions between sympatric mammalian mesocarnivores in Southwestern Europe.

Conclusions

With this wok we provided relevant contributions for the understanding of the carnivore communities in southwestern Europe from a methodological and ecological level. The following main conclusions could be drawn from the work developed:

i.   Although several attractants may be used for species-specific studies in European carnivore communities, Lynx (*Lynx lynx* or *Lynx pardinus*) urine showed the most efficient results for community-wide surveys. Furthermore, lynx urine and Valerian extract provide complementary effectiveness in the attraction of European mammalian carnivores, and elicit investigative behaviour and rubbing responses in Iberian wolves, European wildcats, Eurasian badgers, polecats and red foxes.

ii. While eliciting rubbing behaviour in enclosure trials, the low detectability of hair-snares when compared to camera traps suggest that this behaviour must not be strong under natural conditions. Consequently, this method may not be efficient for short-term occupancy studies of Iberian mesocarnivore populations. Nevertheless, hair collection structures may enable long-term monitoring of mammalian carnivores using a combination of adequate sampling designs and molecular analyses of DNA extracted from the collected biological samples. Particularly, the detectability rates of red foxes in midrank density situations suggest that hair snares could be useful for monitoring of red fox populations.

iii. Our results highlight the potential errors of traditional scat-based sampling methods. The accuracy of species assignment of scats based on their morphology is highly variable (ranging from 0 to 95%) and depends on the abundance of target and other ecologically similar species, and on context-specific circumstances. Such variability prevents extrapolation of accuracy rates over areas, and stresses the importance of using genetic methods for assigning species identifications to scats in order to adequately draw inferences from the patterns observed in nature.

iv. Mammalian mesocarnivores in the Iberian Peninsula are predominantly nocturnal, displaying a high overlap with the activity patterns of murid rodents and partially with European rabbits. The high overlap between the activity patterns of mammalian mesocarnivores and their prey is in accordance with optimal foraging theory, suggesting that

predators forage when they can maximize accessibility to the most profitable prey.

v. Mammalian mesocarnivores, as a community, exhibit a high activity overlap with that of murid rodents, even when a more profitable prey (the European rabbit) is available. This fact appears to be linked either to temporal restrictions imposed by intraguild competitors, or to a balance between an adequate access to European rabbits during a suboptimal period and accessibility to rodent prey.

vi. Three distinct groups of Iberian mesocarnivores could be identified regarding their activity patterns: strictly nocturnal, facultative nocturnal and strictly diurnal species. The first group includes the stone marten, Eurasian badger and common genet, and consists of species that reveal particularly strong selection indices towards nighttime, with little activity during the twilight periods, and strongly avoid being active during daytime. The second group includes the red fox, European wildcat, pine marten and Iberian lynx, and consists of species that positively select nighttime, but also use the twilight periods as expected by chance. Daytime is used less than expected by chance, but is not strictly avoided. The Egyptian mongoose was the only strictly diurnal species.

vii. Activity patterns exhibited by mesocarnivores are not constant among study areas or seasons, suggesting behavioural adjustments to local conditions, probably facilitating coexistence. However, the activity shifts observed were contained within the preferred parts each species' daily cycle, supporting an endogenous regulation of their diel activities. This regulation appears to be particularly constraining in stone martens, common genets and Eurasian badgers.

viii. Segregation along the temporal niche constitutes a recurrent strategy among co-occurring Iberian mesocarnivores. This behaviour appears to facilitate carnivores' coexistence and is more pronounced in more complex communities.

ix. Adjustments along the spatial dimension of the ecological niche are not a frequent strategy among co-occurring similar sized mesocarnivores in the Iberian Peninsula. Such adjustments only occur in asymmetrical competitive relations, where the dominant species is clearly defined, as is the case of the Iberian lynx and the red fox.

x. We found no evidence that similar sized mesocarnivores segregate spatially in mesocarnivore-dominated communities. However, behavioural responses take place in areas of co-occurrence, where subordinate species may adopt a more elusive behaviour. In these situations, potentially stressful interactions are preferably handled by displacements along the temporal and trophic niche dimensions, allowing sympatric intraguild competitors to spatially co-occur.

xi. In the study area where we were able to evaluate the niche relations between the two marten species (PGNP), the stone marten appears to be the dominant competitor over the pine marten, contrasting to what has been reported in other areas of sympatry. This observation suggests that, in similar sized competitors, the relative dominance position is not constant and may change due to context-specific factors.

xii. The interactions between co-occurring Iberian terrestrial carnivores are dynamic, and their strength and direction may vary seasonally and geographically, fact that should be taken into account in community-wide studies.

xiii. Intraguild interspecific interactions significantly influence the spatial, temporal and trophic expression of a species ecological niche, and therefore must be accounted for in species-specific studies.

Acknowledgements

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