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Living with roommates in a shared den: Spatial and temporal segregation among semifossorial mammals

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ABSTRACT

Positive interspecific interactions in animal communities (*i.e.* den sharing) have long been overlooked in animal ecology. The assessment of spatiotemporal overlap among species living within the same burrow system is paramount to explain their strategies of interspecific coexistence. We studied spatiotemporal behavioural patterns of coexistence among four den-sharing mammal species (*i.e.* the crested porcupine *Hystrix cristata*, the Eurasian badger *Meles meles*, the red fox *Vulpes vulpes* and the European pine marten *Martes martes*), inhabiting a hilly area of central Italy. Intensive camera trapping (September 2015-September 2018) was used to estimate the interspecific overlap of both temporal and spatial activity patterns for all species combinations. An extensive nocturnal temporal overlap was recorded among all the species, except the diurnal pine marten. However, crested porcupines were mostly active in the darkest nights, whereas bright moonlight enhanced the hunting success of the red fox. Activity of badgers was limited in bright nights only during cold months, when predation pressure and poaching risk were the highest. Crested porcupines avoided spatial sharing outside the den with both nocturnal carnivores, particularly during the winter, when its cubs are in the den. Overlap in ranging areas and activity rhythms between the red fox and the Eurasian badger may be promoted by a remarkable food niche partitioning. Conversely, spatiotemporal overlap between red foxes and pine martens suggested a significant interspecific spatial partitioning, due to the overlap in feeding habits. Den-sharing represents a form of positive interspecific interaction which may limit energy waste and increase local species diversity and densities. Species using the same burrow system may show both spatial and temporal niche partitioning throughout the year, thus allowing a non-competitive coexistence.

1. Introduction

Species coexistence in ecological communities is mostly influenced by mechanisms of intraspecific competition, predation and niche partitioning (*e.g.* Tannerfeldt et al., 2002; Broekhuis et al., 2018; Tilman and Kareiva, 2018). These factors may in turn affect spatiotemporal behaviour of animal species ranging on the same study area (Savino and Stein, 1982; Cozzi et al., 2012; Kohl et al., 2018). In particular, predator species modulate their behaviour to increase their hunting success, balancing costs and benefits and often forcing most prey species to be active in concealed habitats and in the darkest nights, where and when their detection probability is the lowest (*e.g.* Bowman and Harris, 1980; Lima and Dill, 1990; Fattorini and Pokheral, 2012; Prugh and Golden, 2014). Species sharing the same spatial and temporal behaviour may compete for food, if diet partitioning does not occur (cf. Ciampalini and Lovari, 1985; Patalano and Lovari, 1993), as well as for shelter sites (*e.g.* Richards and Cobb, 1986; Sullivan and Wilson, 2001; Glen and Dickman, 2008).

Dens and den systems (named “setts”) are important refuge to protect vertebrate species from predation (mostly on cubs) and as a buffer against extreme temperatures (Kinlaw, 1999; Roper et al., 2001; Monetti et al., 2005; Mukherjee et al., 2017a, 2017b; Dawson et al., 2019), allowing a safe and successful reproduction (Butler and Roper, 1996; Mori et al., 2016; Mukherjee et al., 2018). Primary excavators directly dig burrows and include both strictly fossorial species (*e.g.* moles *Talpa* spp. and mole rats *Nannospalax* spp.), and semifossorial ones (*i.e.* the Savi’s pine vole *Microtus savii*, the Eurasian badger *Meles meles* and the crested porcupine *Hystrix cristata*). Secondary modifiers, including all the semifossorial mammals, modify and occupy existing burrows. To conclude, simple burrow dwellers (*e.g.* the black footed

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ferret *Mustela nigripes*, martens *Martes* spp., the burrowing owl *Athene cunicularia* and the pine snake *Pituophis melanoleucus*) only use burrows without adding modifications (Campbell and Clark, 1981; Clark et al., 1982; Kinlaw, 1999; Monetti et al., 2005; Mukherjee et al., 2017a). Digging burrows require high costs for semifossorial mammals (*e.g.* Covell et al., 1996; Zelová et al., 2010). Therefore, where natural dens are abundant (*e.g.* caves in calcareous areas, rocky areas, archaeological sites and abandoned mines), single den setts are often used by single species in family groups (*i.e.* up to 30 individuals: Kruuk, 1989; Monetti et al., 2005; Mori et al., 2018; Dorning and Harris, 2019). Conversely, interspecific vertebrate aggregations within the same sett may occur in deciduous woodlands and in the surroundings of urban areas, *i.e.* where dens represent a limiting resource, as well as where density of semi-fossorial species is high (Campbell and Clark, 1981; Pigozzi, 1986; Covell et al., 1996; Mori et al., 2015; Mukherjee et al., 2017a). These facilitative interactions might occur as dens are often constituted by multiple entrances and multiple chambers, which may allow interspecific coexistence (Kruuk, 1989; Kowalczyk et al., 2008; Mori et al., 2015). Patterns of spatiotemporal behavioral overlap among species sharing the same den sett have never been analysed in depth. For instance, crested porcupines may share their dens with at least four other medium-sized mammal species in Italy, including the Eurasian badger, the red fox *Vulpes vulpes* and the European pine marten *Martes martes* (Mori et al., 2015). Interspecific den sharing may occur throughout the year, but crested porcupines have been reported to force other species to move towards alternative setts when their cubs are in the den (Mori et al., 2015, 2016). In Italy, the birth peak in porcupines occurs in late winter (late February- early March: Santini, 1980; Mori et al., 2016). The red fox may represent a predator for porcupine cubs (Lucherini et al., 1995), thus forcing adult paired porcupines to alternate at their dens and to be particularly aggressive to defend offspring (Mori et al., 2014a). Therefore, given that behavioural interference has been observed among species sharing the same setts, a spatiotemporal behavioural segregation may also occur, together with trophic niche partitioning (*e.g.* among foxes and badgers: Ciampalini and Lovari, 1985; among foxes and martens: Goszczyński, 1986; diet of porcupines mainly consists of underground storage organs: Bruno and Riccardi, 1995; Mori et al., 2017). Following the review by Prugh and Golden (2014), for instance, carnivores (*i.e.* the red fox and the mustelids) should be mostly active in moonlight nights; thus, the crested porcupine, a prey species, has been reported to be more active in the darkest nights (Mori et al., 2014b).

In our work, we studied the spatiotemporal mechanisms of coexistence in a community of mammals sharing den setts in central Italy, through an intensive camera-trapping project. We predicted that: (*i*) crested porcupines and den-sharing mesocarnivores would shape their spatiotemporal behaviour to enhance their coexistence; (*ii*) nocturnal mesocarnivores would be more active during bright moonlight nights (cf. Prugh and Golden, 2014).

2. Materials and methods

2.1. Study area

Our survey was conducted in the north-eastern part of the province of Grosseto, central Italy (Poggi di Prata: 43.08 N, 10.099 E; 1350 ha, 475–903 m a.s.l.: Fig. 1).

Over 65% of the study area was covered with deciduous woodlands (mostly *Quercus cerris, Castanea sativa, Ostrya carpinifolia* and *Carpinus betulus*). The Mediterranean macchia (*Juniperus communis*, *Rubus ulmifolius* and *Spartium junceum*: about 1.7%) created a belt around the woodland. Fallows and cultivations (sunflowers, cereals and vegetable gardens) covered about 19.5% **and** 7.8%, respectively. Coniferous woodlands and human settlements (including the villages of Prata and Il Gabellino) covered the remaining part of the study area (Mori et al., 2018). During our survey period, average annual rainfall was 691 ± 34 mm, with three episodes of winter snowfall. Average annual temperature was 15.3 °C, with summer peaks up to 30 °C.

2.2. Camera-trapping

Camera-trapping data were collected in a four-year mammal survey (September 2015–September 2018). We used four (Ziboni Tecnofauna Explorer Case 1988) and three (Multipir 12) camera traps ($N_{TOT} = 7$ camera traps), rotated throughout the study area. Camera traps were located to cover all the habitat types in the study area, along the main paths located in the immediate surroundings of the den entrance (Mori et al., 2016), 20–50 cm above the ground level. The survey involved 2722 trap nights at 25 trap sites, evenly distributed throughout the study area. Each camera trap site was kept active for at least 25 nights, 24 h/day, to take 3 pictures/event. Camera traps were checked at least once every 10 days, to download photos and recharge batteries.

2.3. Spatiotemporal overlap analysis

Interspecific temporal overlaps were calculated between species pairs by considering the time each photo/video was taken. We identified a cold (October-March: mean temperature, 8.9 ± 2.9 °C) and a warm (April–September: mean temperature, 17.2 ± 4.7 °C) period (Mori et al., 2014b). All records of the same species occurring in < 30 min per site were deleted from the final dataset to avoid pseudo-replications (Meredith and Ridout, 2014).

We calculated the interspecific temporal overlap for all the pairwise species, and for both cold and warm periods (as well as for the total annual period), with the R package *overlap* (Meredith and Ridout, 2014), to estimate the coefficient of overlapping (Δ_4: 0, no overlap → 1, total overlap: Linkie and Ridout, 2011; Meredith and Ridout, 2014) between temporal activity patterns all pairwise species combinations. We ranked the temporal overlap of activity patterns following Monterroso et al. (2014), *i.e.* considering a high overlap with $\Delta_4 > 0.75$, a moderate overlap if $0.50 < \Delta_4 < 0.75$ and a low overlap if $\Delta_4 < 0.50$.

We performed Mardia-Watson-Wheeler tests (W) to compare the circadian distribution of each species pair, as a complementary analysis to the estimation of the coefficient of overlapping (Massara et al., 2018).

Moonlight variation has been reported over the 29 days of the lunar cycle (Mori et al., 2014b; Mazza and Mori, 2017), to assess if it affects the temporal pattern of activity of nocturnal mammals. Moon phases were classified as follows: phase (*1*) from new moon to ¼; (N = 695 nights); phase (*2*) from ¼ to ½ (N = 690 nights); phase (*3*) from ½ to ¾ (N = 672 nights) and phase (*4*) over ¾ and full moon (N = 665 nights). Circular statistics (Rayleigh test) were used to assess whether the nocturnal activity of each species was related to moon phase, through the R package *CircStat* (Agostinelli, 2009). Rayleigh tests were also conducted to assess whether each species exhibited random (*i.e.* cathemeral) activity patterns over a 24 h cycle (*e.g.* Pratas-Santiago et al., 2016).

Spatial overlap among den-sharing species was estimated by calculating the Pianka index (0, no overlap → 1, total overlap: Pianka, 1974), considering the proportion of records of each species in different camera trapping stations. We calculated the Pianka index following the formula $O_{jk} = (\Sigma p_{ij} * p_{ik})/(\Sigma p_{ij}^2 * \Sigma p_{ik}^2)^{1/2}$, where p_{ij} is the percentage of records of species *j* and p_{ik} is the proportion of records of the species *k*.

3. Results

A high overlap was observed amongst pairwise comparison of temporal activity rhythms of crested porcupines, Eurasian badgers and red foxes (Fig. 2; Tables 1 and 2). The pine marten was the only diurnal-crepuscular species showing a moderate temporal overlap with other species. The Mardia-Watson-Wheeler tests showed significant dissimilarities between the daily distributions of records of the pine marten

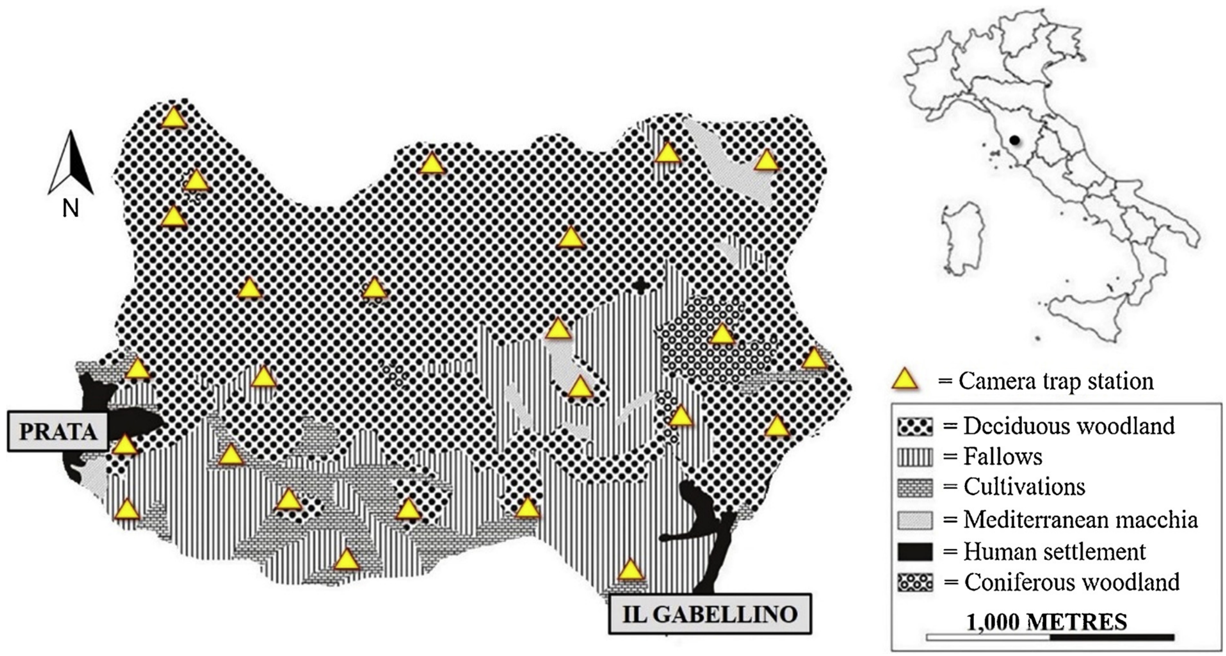

Fig. 1. Location, camera trap stations and habitat type composition of the study area. Villages of Prata and Il Gabellino are reported.

and other species (W = 3.35–4.85; d.f. = 2; P = 0.036 – 0.042: Fig. 2). Conversely, no significant differences were recorded in each species pair comparison (W = 9.42–16.31; d.f. = 2; P = 0.088 – 0.159: Fig. 2). The crested porcupine avoided moonlit nights throughout the year. Eurasian badgers avoided moonlight only in cold months, while in warm ones, activity patterns were irrespective to moon phase. Conversely, the red fox was mostly active in moonlit nights, throughout the year (Table 3). Spatial overlap among porcupines and nocturnal mammals was high in warm months, while being low in cold ones (Fig. 3). Spatial overlap between the red fox and the pine marten remained low throughout the year (Fig. 3).

Table 1
Coefficients of overlapping of activity patterns among den-sharing mammals in the warm and cold periods, and throughout the study period.

Species pairs	Coefficient of overlapping (Δ_4)		
	Cold period	Warm period	Annual
Crested porcupine – Eurasian badger	0.82	0.81	0.84
Crested porcupine – Red fox	0.73	0.82	0.78
Crested porcupine – Pine marten	0.62	0.50	0.63
Eurasian badger – Red fox	0.78	0.90	0.84
Eurasian badger – Pine marten	0.53	0.58	0.56
Red fox – Pine marten	0.64	0.58	0.62

4. Discussion

In our work, we observed a remarkable temporal overlap among temporal activity patterns of crested porcupines, red foxes and Eurasian badgers, all being mostly nocturnal with limited diurnal activity (*e.g.* Corsini et al., 1995; Torretta et al., 2016). Conversely, the pine marten was confirmed to be mostly a diurnal species in Italy (Torretta et al., 2017), thus temporally avoiding all the other species sharing the same den.

However, when temporal overlap was analysed in terms of moon

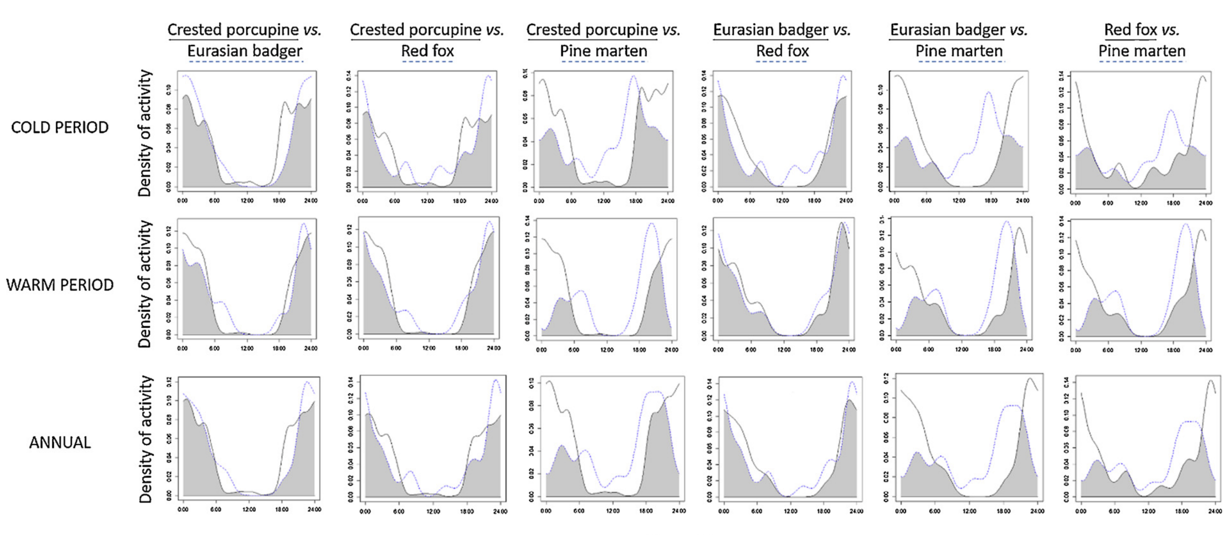

Fig. 2. Overlap of temporal activity patterns among den-sharing mammals.

Table 2
Peaks of activity for each nocturnal mammal species expressed through the Rayleigh test (Z); CI, confidence interval around the mean direction (i.e. hour of activity peak).

Species	Period	Mean direction	CI	Z	*P*
Crested porcupine	Warm	00:28	0.09	6.18	< 0.005
	Cold	01:55	0.11	29.29	< 0.001
	Annual	01:11	0.08	31.05	< 0.001
Eurasian badger	Warm	22:28	0.05	2.14	< 0.001
	Cold	00:08	0.06	25.90	< 0.001
	Annual	23:13	0.08	15.77	< 0.005
Red fox	Warm	23:24	0.04	28.54	< 0.001
	Cold	00:17	0.11	45.12	< 0.001
	Annual	23:45	0.09	36.28	< 0.001
Pine marten	Warm	18:51	0.18	45.58	0.032
	Cold	17:26	0.22	39.55	0.001
	Annual	18.02	0.20	54.13	0.018

Table 3
Peaks of inactivity for each nocturnal mammal species (all but for the pine marten), calculated through circular statistics (Rayleigh test).

	Peak of inactivity				Rayleigh test	
Species	Period	Day	r	Moon phase	Z	*P*
Crested porcupine	Warm	13.8 ± 2.7	0.18	4	5.92	< 0.005
	Cold	16.3 ± 0.9	0.49	4	46.05	< 0.001
Eurasian badger	Warm	8.3 ± 0.6	0.33	3	1.96	0.151
	Cold	15.6 ± 1.4	0.22	4	27.58	< 0.001
Red fox	Warm	4.3 ± 1.1	0.33	1	32.03	< 0.001
	Cold	27.3 ± 3.2	0.44	1	45.12	< 0.001

phases, we observed a niche segregation also between the crested porcupine, mostly active in dark nights (cf. Mori et al., 2014b; Mukherjee et al., 2018), and its main local predator (Lucherini et al., 1995), the red fox, which increased its activity patterns in bright moonlit nights (cf. Penteriani et al., 2013). Conversely, the temporal behaviour of the badger in relation to moon phases was different between the cold and the warm periods, avoiding the moonlight only in the former. During the winter period, the badger is reported as a potential, although rare, prey of the grey wolf *Canis lupus* in the study site (Battocchio et al., 2017). Furthermore, in cold months, the Eurasian badger shifts its diet towards cultivated fruits, e.g. olives (Rosalino et al., 2005a), which may increase the risk of poaching (see Revilla et al., 2001). In warm months, insects and earthworms build up the diet of the Eurasian badger in Mediterranean countries (Ciampalini and Lovari, 1985; Rosalino et al., 2005a). Thus, concentrating ranging movements in dark nights or concealed habitats in cold months may limit predation by large carnivores and visibility to humans, i.e. poaching pressure (cf. Lovari et al., 2017).

In cold months, the crested porcupine highly reduced its spatial overlap with both the red fox and the Eurasian badger. Accordingly, the birth peak for this large rodent occurs in February (Sonnino, 1998; Mori et al., 2016), and, during this period, porcupines are particularly aggressive and displace all the other den-sharing species from their burrows (cf. Mori et al., 2014a, 2015). Spatial overlap between the crested porcupine and the pine marten remained high as this small carnivore does not represent a predator nor a competitor for the crested porcupine (cf. Biancardi and Rinetti, 2002; Balestrieri et al., 2011). Both species are linked to dense woodland areas and concealed habitats (Storch et al., 1990; Monetti et al., 2005; Pereboom et al., 2008; Balestrieri et al., 2010; Mori et al., 2014c). Furthermore, interspecific encounters are limited by temporal partitioning (*e.g.* Corsini et al., 1995; Mori et al., 2014b; Torretta et al., 2017).

The high annual spatial overlap of movement patterns between the red fox and the Eurasian badger might be promoted by a remarkable trophic niche partitioning (*e.g.* Ciampalini and Lovari, 1985; Canova and Rosa, 1994). Accordingly, red foxes mainly feed on small mammals and birds, whereas badger's diet mostly consists of fruits, insects and earthworms (Marassi and Biancardi, 2002; Rosalino et al., 2005a; Soe et al., 2017). In general, Eurasian badgers have been reported to be dominant competitors over red foxes (Neal and Roper, 1991; Macdonald et al., 2004). However, at shared setts, once it was evident that encounters will not escalate to aggression, each species was unaffected by the presence of the other (Macdonald et al., 2004).

Niche partitioning and temporal segregation may allow also a spatial peaceful coexistence between the badger and the pine marten (Balestrieri et al., 2004; Biancardi and Rinetti, 2002; Marassi and Biancardi, 2002; Balestrieri et al., 2011). Conversely, the low spatio-temporal overlap detected between the pine marten and the red fox may imply a sort of interspecific competition among these carnivores (cf. Palomares and Caro, 1999; Donadio and Buskirk, 2006), possibly due to a high dietary overlap (up to 70%: Storch et al., 1990; Baltrūnaitė, 2002).

Den-sharing represents a form of positive interspecific interaction, which may limit energy waste and stress. Den sites are often reported to represent a limiting resource, thus promoting interspecific sharing, when possible (Fernández and Palomares, 2000; Revilla et al., 2001; Rosalino et al., 2005b). This positive interaction may also increase local species diversity, i.e. promoting the range expansion and dispersal of both native and alien species (Hacker and Gaines, 1997; Kowalczyk

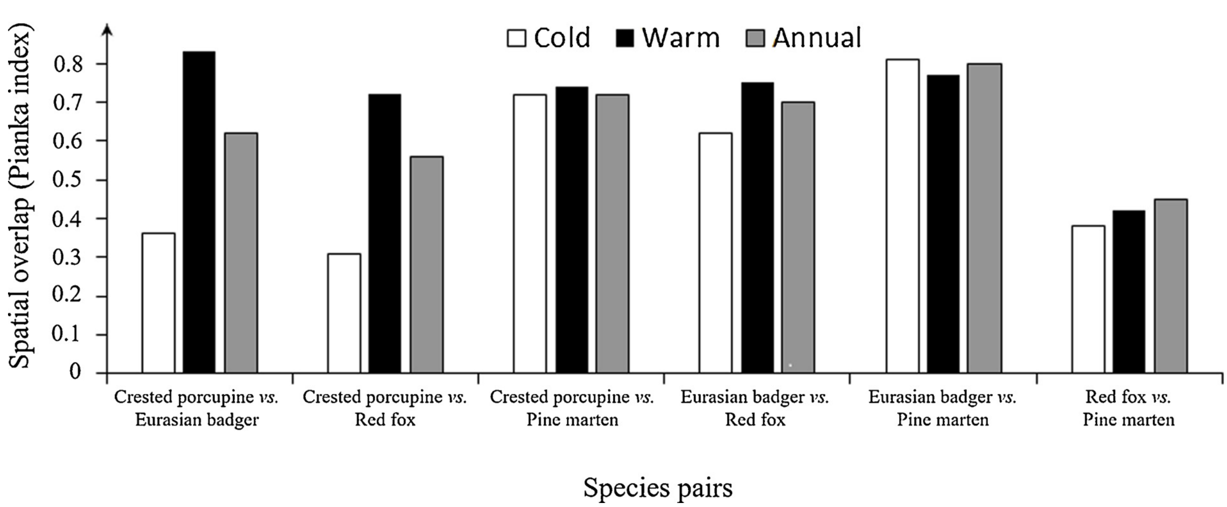

Fig. 3. Spatial overlap coefficients among den-sharing mammals (crested porcupine, Eurasian badger, red fox and pine marten) in the warm and cold periods, and throughout the study period.

et al., 2008; Geiger et al., 2018). Species using the same den sett may show both spatial and temporal niche partitioning throughout the year, thus allowing a non-competitive coexistence. Further studies are needed to assess the chamber organization and sharing within den setts, to clarify whether different species are present at different depths within the same sett (cf. Bassano and Peracino, 1997).

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References

Agostinelli, C., 2009. CircStats: Circular Statistics, From Topics in Circular Statistics (2001) R Package Version 0. Available from: http://CRAN.R-project.org/package=CircStats. Accessed on 19 January 2019. .
Balestrieri, A., Remonti, L., Prigioni, C., 2004. Diet of the Eurasian badger (*Meles meles*) in an agricultural riverine habitat (NW Italy). Hystrix 15, 3–12.
Balestrieri, A., Remonti, L., Ruiz-González, A., Gómez-Moliner, B.J., Vergara, M., Prigioni, C., 2010. Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mammal. Biol. 75, 412–419.
Balestrieri, A., Remonti, L., Ruiz-González, A., Vergara, M., Capelli, E., Gómez-Moliner, B.J., Prigioni, C., 2011. Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). Acta Theriol. 56, 199–207.
Baltrūnaitè, L., 2002. Feeding habits, food niche ovelap of red fox (*Vulpes vulpes* L.) and pine marten (*Martes martes* L.) in hilly moraine highland, Lith. Ekologija 2, 27–32.
Bassano, B., Peracino, V., 1997. A robotized system for exploring mammal burrows. Wildl. Soc. Bull. 25, 98–100.
Battocchio, D., Iacolina, L., Canu, A., Mori, E., 2017. How much does it cost to look like a pig in a wild boar group? Behav. Proc. 138, 123–126.
Biancardi, C.M., Rinetti, L., 2002. Alimentazione della martora *Martes martes* (L., 1758) (Mammalia, Mustelidae) nell'Alto Luinese (Italia settentrionale). Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat. Milano 142, 165–172.
Bowman, G.B., Harris, L.D., 1980. Effect of spatial heterogeneity on ground-nest depredation. J. Wildl. Manage. 44, 806–813.
Broekhuis, F., Thuo, D., Hayward, M.W., 2018. Feeding ecology of cheetahs in the Maasai Mara, kenya and the potential for intra-and interspecific competition. J. Zool. (Lond.) 304, 65–72.
Bruno, E., Riccardi, C., 1995. The diet of the crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area. Zeitsch. Säugetierk 60, 226–236.
Butler, J.M., Roper, T.J., 1996. Ectoparasites and sett use in European badgers. Anim. Behav. 52, 621–629.
Campbell, T.M., Clark, T.W., 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. Am. Midl. Nat. 105, 269–276.
Canova, L., Rosa, P., 1994. Badger *Meles meles* and fox *Vulpes vulpes* food in agricultural land in the Western Po plain (Italy). Hystrix 5, 73–78.
Ciampalini, B., Lovari, S., 1985. Food habits and trophic niche overlap of the badger (*Meles meles* L.) and the Red fox (*Vulpes vulpes* L.) in a Mediterranean costalarea. Zeitschr. Saugetier 50, 226–234.
Clark, T.W., Campbell III, T.M., Socha, D.G., Casey, D.E., 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Nat. 42, 572–582.
Corsini, M.T., Lovari, S., Sonnino, S., 1995. Temporal activity patterns of crested porcupines Hystrix cristata. J. Zool. (Lond.) 236, 43–54.
Covell, D.F., Miller, D.S., Karasov, W.H., 1996. Cost of locomotion and daily energy expenditure by free-living swift foxes (*Vulpes velox*): a seasonal comparison. Can. J. Zool. 74, 283–290.
Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W., Schmid, B., 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology 93, 2590–2599.
Dawson, S.J., Broussard, L., Adams, P.J., Moseby, K.E., Waddington, K.I., Kobryn, H.T., Bateman, P.W., Fleming, P.A., 2019. An outback basis: the ecological importance of bilby burrows. J. Zool. (Lond.). https://doi.org/10.1111/jzo.12663.
Donadio, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in Carnivora. Am. Nat. 167, 524–536.
Dorning, J., Harris, S., 2019. Quantifying group size in the red fox: impacts of definition, season and intrusion by non-residents. J. Zool. (Lond.). https://doi.org/10.1111/jzo.12650. https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.12650.
Fattorini, N., Pokheral, C.P., 2012. Activity and habitat selection of the Indian crested porcupine. Ethol. Ecol. Evol. 24, 377–387.
Fernández, N., Palomares, F., 2000. The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation. Biol. Conserv. 94, 51–61.
Geiger, M., Taucher, A.L., Gloor, S., Hegglin, D., Bontadina, F., 2018. In the footsteps of city foxes: evidence for a rise of urban badger populations in Switzerland. Hystrix 29, 236–238.
Glen, A.S., Dickman, C.R., 2008. Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? J. Appl. Ecol. 45, 700–707.
Goszczyński, J., 1986. Diet of foxes and martens in central Poland. Acta Theriol. 31, 491–506.
Hacker, S.D., Gaines, S.D., 1997. Some implications of direct positive interactions for community species diversity. Ecology 78, 1990–2003.
Kinlaw, A.L., 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. J. Arid Environ. 41, 127–145.
Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W., MacNulty, D.R., 2018. Diel predator activity drives a dynamic landscape of fear. Ecol. Monogr. 88, 638–652.
Kowalczyk, R., Jędrzejewska, B., Zalewski, A., Jędrzejewski, W., 2008. Facilitative interactions between the Eurasian badger (*Meles meles*), the red fox (*Vulpes vulpes*) and the invasive raccoon dog (*Nyctereutes procyonoides*) in the Bialowieza Primeval Forest, Poland. Can. J. Zool. 86, 1389–1396.
Kruuk, H., 1989. The Social Badger. Oxford University Press, Oxford, UK.
Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.
Linkie, M., Ridout, M.S., 2011. Assessing tiger-prey interactions in Sumatran rainforests. J. Zool. (Lond.) 284, 224–229.
Lovari, S., Corsini, M.T., Guazzini, B., Romeo, G., Mori, E., 2017. Suburban ecology of the crested porcupine in a heavily poached area: a global approach. Eur. J. Wildl. Res. 63, 10.
Lucherini, M., Lovari, S., Crema, G., 1995. Habitat use and ranging behaviour of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: is shelter availability a key factor? J. Zool. (Lond.) 237, 577–591.
Macdonald, D.W., Buesching, C.D., Stopka, P., Henderson, J., Ellwood, S.A., Baker, S.E., 2004. Encounters between two sympatric carnivores: red foxes (*Vulpes vulpes*) and European badgers (*Meles meles*). J. Zool. (Lond.) 263, 385–392.
Marassi, M., Biancardi, C.M., 2002. Diet of the Eurasian badger (*Meles meles*) in an area of the Italian prealps. Hystrix 13, 19–28.
Massara, R.L., Paschoal, A.M.O., Bailey, L.L., Doherty Jr., P.F., Barreto, M.F., Chiarello, A.G., 2018. Effect of humans and pumas on the temporal activity of ocelots in protected areas of Atlantic Forest. Mammal. Biol. 92, 86–93.
Mazza, G., Mori, E., 2017. Activity rhythms of the Eurasian badger in relation to moon phases. Atti Del XXVII Convegno Della Società Italiana Di Etologia 36.
Meredith, M., Ridout, M., 2014. Overview of the Overlap Package. Available from: http://cran.cs.wwu.edu/web/packages/overlap/vignettes/overlap.pdf. (Accessed on 23 December 2018). .
Monetti, L., Massolo, A., Sforzi, A., Lovari, S., 2005. Site selection and fidelity by crested porcupine for denning. Ethol. Ecol. Evol. 17, 149–159.
Monterroso, P., Alves, P.C., Ferreras, P., 2014. Plasticity in circadian activity patterns of mesocarnivores in southwestern Europe: implications for species coexistence. Behav. Ecol. Sociobiol. 68, 1403–1417.
Mori, E., Maggini, I., Menchetti, M., 2014a. When quills kill: the defense strategy of the crested porcupine *Hystrix cristata* L., 1758. Mammalia 78, 229–234.
Mori, E., Nourisson, D.H., Lovari, S., Romeo, G., Sforzi, A., 2014b. Self-defence may not be enough: moonlight avoidance in a large, spiny rodent. J. Zool. (Lond.) 294, 31–40.
Mori, E., Lovari, S., Sforzi, A., Romeo, G., Pisani, C., Massolo, A., Fattorini, L., 2014c. Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. Behav. Proc. 107, 112–118.
Mori, E., Menchetti, M., Balestrieri, A., 2015. Interspecific den sharing: a study on European badger setts using camera traps. Acta Ethol. 18, 121–126.
Mori, E., Menchetti, M., Lucherini, M., Sforzi, A., Lovari, S., 2016. Timing of reproduction and paternal cares in the crested porcupine. Mammal. Biol. 81, 345–349.
Mori, E., Bozzi, R., Laurenzi, A., 2017. Feeding habits of the crested porcupine *Hystrix cristata* L. 1758 (Mammalia, Rodentia) in a Mediterranean area of Central Italy. Eur. Zool. J. 84, 261–265.
Mori, E., Lovari, S., Mazza, G., 2018. The bone collector: temporal patterns of bone-gnawing behaviour define osteophagia as a female prerogative in a large rodent. Behav. Ecol. Sociobiol. 72, 89.
Mukherjee, A., Pilakandy, R., Kumara, H.N., Manchi, S.S., Bhupathy, S., 2017a. Burrow characteristics and its importance in occupancy of burrow dwelling vertebrates in semiarid area of Keoladeo National Park, Rajasthan, India. J. Arid Environ. 141, 7–15.
Mukherjee, A., Kumara, H.N., Bhupathy, S., 2017b. Determinants of occupancy and burrow site selection by Indian crested porcupine in Keoladeo National Park, Bharaptur, Rajasthan, India. Curr. Sci. 112, 2440–2448.
Mukherjee, A., Kumara, H.N., Bhupathy, S., 2018. Environmental determinants of activity variation of an overlooked burrowing rodent: the Indian crested porcupine. Mammalia 82, 449–459.
Neal, E., Roper, T.J., 1991. The environmental impact of badgers (*Meles meles*) and their setts. Symp. Zool. Soc. Lond. 63, 89–106.
Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. Am. Nat. 153, 492–508.
Patalano, M., Lovari, S., 1993. Food habits and trophic niche overlap of the wolf *Canis lupus*, L. 1758 and the red fox *Vulpes vulpes* (L. 1758) in a Mediterranean mountain area. Rev. Ecol. Terre Vie 48, 279–294.
Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palmares, F., Lopez-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L., Lourenço, R.,

2013. Responses of a top and meso predator and their prey to the moon phases. Oecologia 173, 753–766.

Pereboom, V., Mergey, M., Villerette, N., Helder, R., Gerard, J.F., Lode, T., 2008. Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. Can. J. Zool. 86, 983–991.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. U. S. A. 71, 2141–2145.

Pigozzi, G., 1986. Crested porcupines *Hystrix cristata* within badger setts *Meles meles* in the Maremma Natural Park, central Italy. Saugetierkd. Mitt. Band 33, 261–263.

Pratas-Santiago, L.P., Gonçalves, A.L.S., da Maia Soares, A.M.V., Spironello, W.R., 2016. The moon cycle on the activity patterns of ocelots and their prey. J. Zool. (Lond.) 299, 275–283.

Prugh, L.R., Golden, C.D., 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J. Anim. Ecol. 83, 504–514.

Revilla, E., Palomares, F., Fernández, N., 2001. Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. J. Zool. (Lond.) 255, 291–299.

Richards, R.A., Cobb, J.S., 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. Can. J. Fish. Aquat. Sci. 43, 2250–2255.

Roper, T.J., Ostler, J.R., Schmid, T.K., Christian, S., 2001. Sett use in European badgers Meles meles. Behavior 138, 173–187.

Rosalino, L.M., Loureiro, F., Macdonald, D.W., Santon-Reis, M., 2005a. Dietary shifts of the badger (*Meles meles*) in Mediterranean woodlands: an opportunistic forager with seasonal specialisms. Mammal. Biol. 70, 12–23.

Rosalino, L.M., Macdonald, D.W., Santos-Reis, M., 2005b. Resource dispersion and badger population density in Mediterranean woodlands: is food, water or geology the limiting factor? Oikos 110, 441–452.

Santini, L., 1980. The habits and influence on the environment of the old world porcupine *Hystrix cristata* L. In the northernmost part of its range. Vert. Pest Conf. Proc. Collection 1, 149–153.

Savino, J.F., Stein, R.A., 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111, 255–266.

Soe, E., Davison, J., Süld, K., Saarma, U., 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. Mamm. Rev. 47, 198–211.

Sonnino, S., 1998. Spatial activity and habitat use of crested porcupine, *Hystrix cristata* L., 1758 (Rodentia, Hystricidae) in central Italy. Mammalia 62, 175–190.

Storch, I., Lindström, E., de Jounge, J., 1990. Diet and habitat selection of the pine marten in relation to competition with the fox. Acta Theriol. 35, 311–320.

Sullivan, W., Wilson, K.J., 2001. Differences in habitat selection between Chatham petrels (*Pterodroma axillaris*) and broad-billed prions (*Pachyptila vittata*): implications for management of burrow competition. New Zeal. J. Ecol. 25, 65–69.

Tannerfeldt, M., Elmhagen, B., Angerbjörn, A., 2002. Exclusion by interference competition? The relationship -between red and arctic foxes. Oecologia 132, 213–220.

Tilman, D., Kareiva, P., 2018. Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions (MPB-30), vol. 30 Princeton University Press, Princeton, New Jersey, USA.

Torretta, E., Serafini, M., Puopolo, F., Schenone, L., 2016. Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (N-W Italy). Acta Ethol. 19, 123–132.

Torretta, E., Mosini, A., Piana, M., Tirozzi, P., Serafini, M., Puopolo, F., Saino, N., Balestrieri, A., 2017. Time partitioning in mesocarnivore communities from different habitats of NW Italy: insights into martens' competitive abilities. Behav. 154, 241–266.

Zelová, J., Šumbera, R., Okrouhlík, J., Burda, H., 2010. Cost of digging is determined by intrinsic factors rather than by substrate quality in two subterranean rodent species. Physiol. Behav. 99, 54–58.