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Spatio-temporal ecology of a carnivore community in middle atlas, NW of Morocco

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ABSTRACT

In species that live in sympatry, some dimensions of their ecological niche can overlap, but coexistence is possible thanks to segregation strategies, being the differential use of space and time one of the most frequent. Through a pioneer study in North-West Africa based on a camera-trapping survey, we studied ecology features of a carnivores' community in the Middle Atlas Mountains, Morocco. We focused on how species shared (or not) the territory and their activity patterns. Camera trapping detected five carnivorous species: African golden wolf (*Canis lupaster*), red fox (*Vulpes vulpes*), domestic dog (*Canis lupus familiaris*), genet (*Genetta genetta*) and African wildcat (*Felis lybica lybica*). Generalized Linear Models confirmed different habitat selection patterns between these species. The presence of a small protected area or prey availability apparently were not determinant factors in the abundance of these species. Spatial segregation patterns were observed between the red fox with the domestic dog and between the red fox with the genet. Kernel density estimates showed strong temporal segregation of red fox and African golden wolf with regard to domestic dog, and suggested avoidance mechanisms for the triad red fox, genet and African golden wolf. Despite the influence of interspecific competition in the assembly of the community, human pressure was apparently the most relevant factor related with the spatio-temporal segregation in this territory.

1. Introduction

The term biological community includes the concept of coexistence between several species in the same ecosystem, each of them adapted to a specific ecological role or niche (Begon et al., 2006). In species that live in sympatry, usually one or several dimensions of the niche (trophic, spatial or temporal) overlap between them, which can generate interspecific competition. However, coexistence is still possible thanks to the many strategies that have been acquired through evolution (Grime and Pierce, 2012). One of the most frequent, the differential use of space and time, occurs especially in those species with similar ecological niches, as it happens within the Carnivora order (e.g. Sarmento et al., 2011; Ferreras et al., 2016; Hearn et al., 2018).

One of the main components in the use of space and time is habitat selection. The most recent habitat definitions, based on the concept of ecological niche, establishes that species choose conditions and resources that allow them to increase their fitness and persist in the ecosystem (Mitchell and Hebblewhite, 2012). The availability of resources, the presence of refuges and the interaction with potential competitors and predators play a fundamental role. Predators tend to choose energy efficient areas, dependent on prey availability or abundance (e.g. Pyke et al., 1977, Gil-Sánchez et al., 1999; Martín-Díaz et al., 2018), as well as with refuges in which they can rest and raise or easily avoid their potential competitors (Begon et al., 2006; Mitchell and Hebblewhite, 2012).

Since the beginning of the 20th century, carnivores have experienced numerous local extinctions and reductions in their geographical range as a result of human activities (Ripple et al., 2014; Aulagnier et al., 2015), with protected areas currently their last refuges (Mills, 1991; Packer et al., 2013). Particularly, in North-West Africa, the enormous human population growth of the last century in Morocco led to degradation of forests and pastures as a result of the irrational use of resources and intense overgrazing (Kouba et al., 2018). To face this ecological problem, the government delimitates the forest estate and provides a legal basis for what is permissible and what is not. This is how small protected areas are created. It is required a special State authorisation for activities

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such as: logging, hunting or grazing. But as we could notice, these measurements are not always accomplished. Despite the efforts of the governments, local extinction of emblematic carnivores seems to have endured since the beginning of the 20th century (Cuzin, 2003; Aulegnier et al., 2017). For instance, the Barbary leopard (*Panthera pardus pardus*) was determined to be extinct in 2016, after an exhaustive 14-year study (Urios and Soria, 2019).

This study aims to investigate the structure and basic functioning of the carnivore community present in the North African mountains of the Middle Atlas, within a study area exactly located where the last evidences of the existence of the Barbary leopard were detected in 2002 (Purroy et al., 2003). More specifically, we seek to investigate: 1) the composition of the carnivore community; 2) the factors that determine habitat selection for each species; 3) the strategies that facilitate the coexistence of the different species of this community, predicting both spatial and time segregations following the competitive exclusion principle (Hardin, 1960); and 4) the effectiveness of a specific small protected area implemented by the Moroccan government.

2. Material and methods

2.1. Study area

The study was conducted in southern Middle Atlas, Morocco, in an area of 3490 ha, located between the small towns of Ercherket, Bou Mia and Tizy N'Isly (32° 23.416′N, 5° 45.268′ W; Fig. 1). The area constitutes a representative zone for north African carnivores, where most of the potential species of the region can be found (Médail and Quézel, 1999; Aulagnier et al., 2015; Aulegnier et al., 2017), including the latest cite of Barbary leopard presence (Purroy et al., 2003; Purroy, 2010). It is a Mediterranean medium mountain landscape (1000−2000 m asl), with steep slopes and calcareous soils, mainly limestones. It presents a temperate and humid climate, with an annual rainfall of 600−1200 mm and an average annual temperature of 10 °C. The vegetation is characterized by mixed meso and supramediterranean forests, composed by oak (*Quercus ilex*), aleppo pine (*Pinus halepensis*), bushy formations of balearic boxwood (*Buxus balearica*), junipers (*Juniperus communis*) and phoenicean juniper (*J. phonicea*) between 1270−1600 m asl. In lower areas, close to the river, it appears a very degraded riverbank forest, dominated by the white poplar (*Populus alba*). Given the proximity of human settlements, the forested area appears patched by cereal crops (*Triticum sp.* and *Secale cereale*) and fruit tree plantations (*Malus sp.*), or are completely bare land due to intense grazing caused by sheep and goats. Within the study area there is a small protected area (1080 ha), bounded by a fence in which human activities such as logging, hunting and grazing are forbidden.

2.2. Field work

First, we've performed a systematic walking survey on the area finding traces of wildlife paths, with leopard as the main target species. Then, we design a non-intrusive sampling based on a remote camera survey (O'Connell et al., 2010), placing a total of 21 passive infrared triggered camera-traps (Moultrie M-999I©) on trails where the main wildlife paths were. The cameras were placed with a distance of 0.5–2.2 km between them (Fig. 1). Following Henschel and Ray (2003) recommendations, the possibility of detecting Barbary leopard implied the placement of 25 camera-traps to cover an area of 100 km^2, with a separation of 2 km between each other.

We placed 10 cameras inside the protected area and the remaining 11 outside of this area (Fig. 1). They were programmed to take three photographs every 10 s, 24 h a day, facilitating independent captures of individuals (O'Connell et al., 2010). As an attractant, we used 1 cm^3 of Iberian lynx urine (*Lynx pardinus*) from the El Acebuche captive breeding centre (Huelva, Spain), which was sprayed directly on the substrate. Lynx urine is widely used as an attractant for carnivores in the Western Mediterranean region, allowing a high capture efficiency with a minimum economic cost (Gil-Sánchez et al., 2011; Monterroso et al., 2011; Jiménez et al., 2017). Every seven days, we verified each device and also sprayed urine in the same spot, avoiding the reduction of its

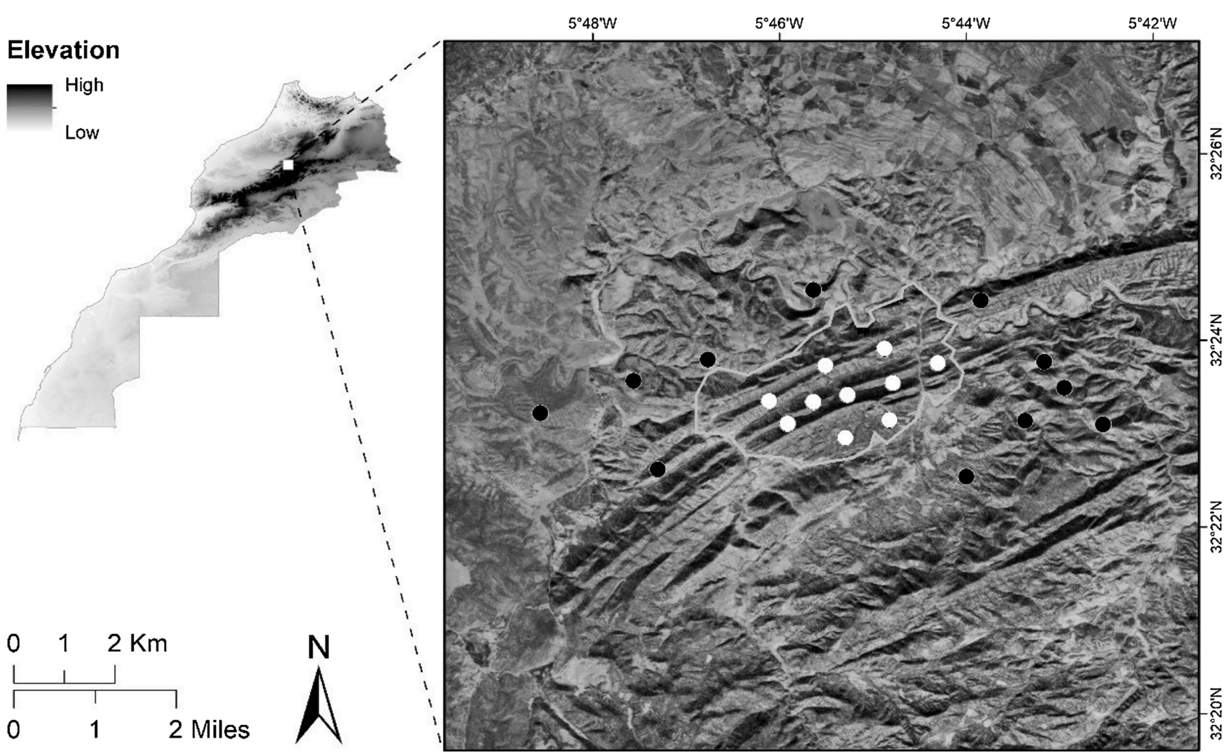

Fig. 1. Location of the study area in Morocco and the remote cameras' distribution. White dots represent the camera-traps located within the protected area (n = 10), while the black dots are the cameras placed outside the protected area (n = 11). The grey line represents the fence that delimitates the protected area.

effectiveness over time. The sampling period ranged from 18th October to 12th December of 2016, with an average activity of each camera trap of 56 days. The total sampling effort was, therefore, 1019 camera-days, as it is recommended in this type of studies (Henschel and Ray, 2003; O'Connell et al., 2010).

3. Data analyses

3.1. Habitat selection patterns

To describe the habitat, we selected twenty environmental variables classified into seven categories (Table 1), which are related to the presence and abundance of carnivores in Mediterranean areas (see e.g. Monterroso et al., 2011; Ferreras et al., 2016). We used the Relative Abundance Index (RAI) to estimate the abundance of people, potential prey, livestock and carnivores, as number of independent captures per 100 camera trap-days (O'Connell et al., 2010). The use of the RAI has been criticized as an inaccurate estimator of the abundance of a species in a specific territory (Mackenzie and Nichols, 2004; Sollmann et al., 2013). However, recently Jiménez et al. (2017) have demonstrated that a positive relationship exists between the RAI and the real density of carnivores in a Mediterranean community (Sup. Mat. 1). In our study, the data variability of the RAI in comparison with the probability of occupancy (ψ, Table 2), allowed us to build stronger models for the habitat selection patterns of the species (Sup. Mat. 2). The criteria established to consider two consecutive captures as independent were: 1) we can recognize images of different individuals or 2) it elapses more than 1 h between images of the same individual or species, when they could not be identified (O'Connell et al., 2010).

The remaining environmental variables were determined with ArcGis 10.2 (ESRI, 2015), using a base map of Morocco. To provide a more complete characterization of the habitat use patterns, the categories of vegetation and topography were calculated at different spatial scales, based on the activity ratios of the carnivores (Hearn et al., 2018; Martín-Díaz et al., 2018). For this, two concentric circles (buffers) were drawn for each camera trap, using its placement point as the centre and taking 1000 m and 250 m as the radii. The availability of water resources and the human impact on the environment (presence of nearby towns, isolated houses, roads and unpaved roads) were calculated as the linear distance from the camera trap to the target variable.

Table 1
Environmental variables selected for the GLM (General Linear Models) performed, in order to know the habitat selection patterns for each species pf the study.

Categories	Environmental variables
Vegetation	% of dense forest % of clear forest % of cultivated land
Topography	Altitude (m) Slope (%)
Water resources availability	Distance to the river (m)
Prey availability	Hare abundance (Independent captures/100 camera trap-days) Micromammals abundance (Independent captures/ 100 camera trap-days)
Location regarding the protected area	Location regarding the protected area (outside = 1, inside = 0)
Humanization degree	People abundance (Independent captures /100 camera trap-days) Livestock abundance (Independent captures /100 camera trap-days) Distance to the nearest town (m) Distance to isolated houses (m) Distance to the nearest paved road (m) Distance to the nearest unpaved road (m)
Another carnivore abundance	African golden Wolf abundance (Independent captures/100 camera trap-days) Red fox abundance (Independent captures/100 camera trap-days) Domestic dog abundance (Independent captures/ 100 camera trap-days) Genet abundance (Independent captures/100 camera trap-days) African wildcat abundance (Independent captures/ 100 camera trap-days)

Table 2
Summary of the camera trapping survey. It includes Relative Abundance Index (RAI) and the occupancy probability (ψ); standard error (SE).

Species	Number of independent captures	% of camera-traps with detections	RAI	ψ
Vulpes vulpes	198	95 %	18.323 (3.962)	0.952 (0.046)
Canis lupaster	26	52 %	2.641 (0.848)	0.649 (0.154)
Genetta genetta	7	24 %	0.669 (0.283)	0.399 (0.224)
Felis lybica lybica	4	19 %	0.274 (0.201)	0.125 (0.097)
Canis lupus familiaris	71	33 %	6.6 (1.683)	0.61 (0.012)
Lepus capensis	106	86 %	9.435 (1.899)	0.81 (0.085)
Micromammals	43	33 %	0.751 (0.347)	0.334 (0.103)

Once all the environmental variables were determined, we made bivariate correlations, discarding redundant variables (R_s with $P < 0.05$) that could imply replication in the subsequent analyses. Thus, the variables proportion of clear forest, proportion of cultivated land and distance to isolated houses were eliminated for the buffer of 250 m and the proportion of cultivated land and altitude for the buffer of 1000 m.

To know the habitat selection patterns for each species, we performed Generalized Linear Models (GLM), using the RAI as the dependent variable and the rest of environmental variables as independent variables. We carried out models for each buffer size (250 m and 1000 m), allowing us to know micro- and macro- scale selection patterns. We chose the best models using the AIC (Akaike Information Criteria) value criteria, identifying first the most parsimonious model, that is, the one that presented the lowest AIC, and then classifying the rest of them regarding this first model. Finally, the AIC difference between the first model and the others (Δ-AIC) was calculated, allowing us to select the models with ΔAIC ≤2, considering that within this range the models are equally plausible (Burnham and Anderson, 2004).

We wanted to focus on the variable "protected area" and its influence on the species' abundance, so we compare the RAI of each species inside and outside of the limits of the protected area (Fig. 2). We tested each difference using the U Mann-Withney test.

3.2. Spatial overlap

The detection histories were created for each carnivore using the camera records, indicating the presence (1) or absence (0) of each of them by camera and day of sampling, being one day the sampling occasion. To determine the probability of occupancy (ψ) of each species in the territory, we used the program PRESENCE v.12 in the modality single species/single season (Mackenzie et al., 2006). Then, we built conditional occupancy models to estimate the effect of the dominant species of the community upon the probability of occupancy and detection of the subordinate ones (Mackenzie et al., 2006). For this, we established a hierarchy by size, in which the domestic dog was dominant against the other three carnivores, the African golden wolf was dominant against the red fox and the genet, and the fox was only dominant against the genet. With the interaction factor (φ) we evaluated the probability of coexistence between dyads of two species in the territory. This factor was calculated under the expression:

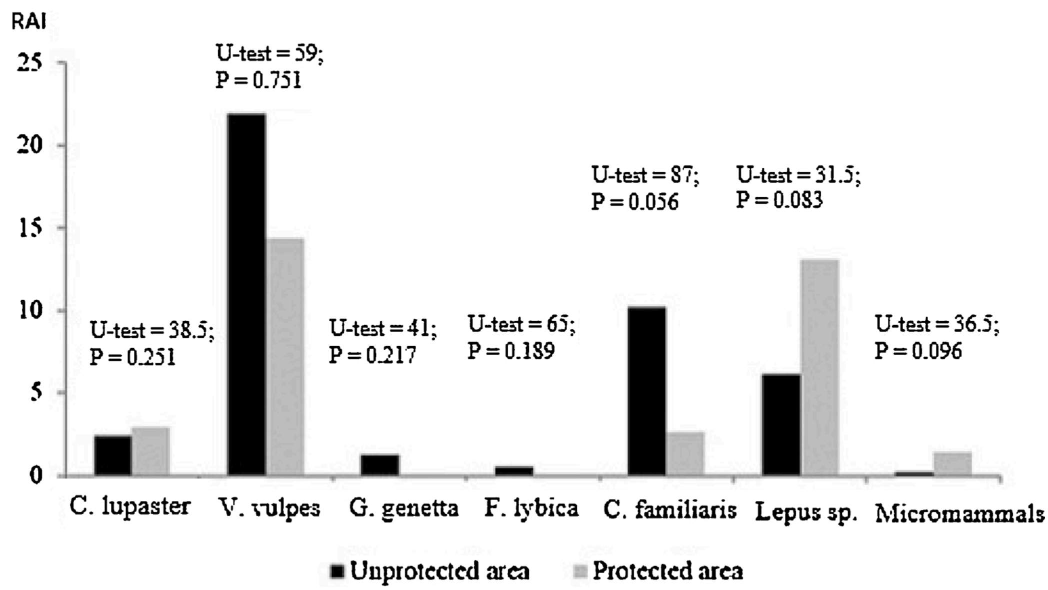

Fig. 2. Relative abundance Index (RAI) of mammals within and outside the area of livestock and hunting exclusion. *U*-tests with *P* levels are shown.

Which can take three ranges of values: values < 1 indicates spatial segregation, values > 1 indicate spatial association and results close to 1 reveals independent distributions (Mackenzie et al., 2006).

3.3. Temporal overlap

The daily activity patterns were studied by Kernel density estimation (Ridout and Linkie, 2009). First, each were studied species independently, and then, we made comparisons between predator-predator and predator-prey patterns using the overlap index (Δ). This overlap coefficient ranges from 0, if the species do not overlap in time, to 1, if the overlap is complete. The index also takes into account the number of detections made. Therefore, for small sample sizes (< 75 detections) it was used the overlap coefficient Δ1, while the Δ4 overlap coefficient was chosen when the detections were > 75.

Both Generalized Linear Models (GLM) and Kernel density analyses were performed with R 3.5.1 (R Core Team, 2018).

4. Results

4.1. Community species composition

The camera-traps took images of five species of carnivores: African golden wolf (*Canis lupaster*), red fox (*Vulpes vulpes*), genet (*Genetta genetta*), North African wildcat (*Felis lybica lybica*) and domestic dog (*Canis lupus familiaris*). We also detected the presence of hares (*Lepus capensis*) and other small rodents' species, that were classified as micromammals. Finally, we found three traces of clear footprints during the field works confirming the presence of the North African caracal (*Caracal caracal algira*) in the area, but it was not captured by the camera-traps, so we did not include it in the study. We could not detect any evidence of leopard presence (Table 2). It is important to highlight that we only used camera-trap records to carry out this study.

4.2. Habitat selection patterns

The GLMs showed different habitat selection patterns for each sampled carnivore. For the African golden wolf, habitat choice preferences varied according to buffer size. Thus, at a micro-scale level (250 m) three models were chosen as equally plausible (Table 3). All the selected variables had a positive influence on the abundance of the African golden wolf, as it can be seen on Table 4. That means that this animal has a preference on dense forest locations, as high as possible and far from human buildings. For the buffer size of 1000 m, only the distance to isolated houses (model A04) seemed to influence the choice of habitat with a positive effect of the variable.

The remaining three species evaluated were related to a single environmental variable, regardless of the buffer size selected. For example, for the red fox the slope was the selected variable (Table 3). However, it was observed a reduction of its importance in the explanation of the model (D^2) when the buffer size was increased. In any case, the slope of the area had a positive influence on the presence of the fox (Table 4).

The distance to the road was the only variable selected for the genet, for both buffer sizes (models G01, G02). This variable had a positive influence in the abundance of the genet (Table 4). As for the domestic

Table 3
Selection of the most parsimonious GLM models (Δ-AICc > 2) for each carnivore species. It is included information about the number of parameters (*k*), the AICc value (Corrected Akaike's Information Criterion) and the deviance (D^2).

Buffer size	Species	Model	Covariable	k	AICc	Δ-AICc	D^2
250 m	*V. vulpes*	V01	Slope	1	172.73	0	51.06
	C. lupaster	A01	% of dense forest + Altitude	2	117.32	0	29.36
		A02	Altitude	1	118.09	0.77	24.63
		A03	% of dense forest + Isolated houses	2	118.83	1.51	25.79
	G. genetta	G01	Distance to the nearest pave road	1	59.45	0	5644
	C. lupus familiaris	CL01	People abundance	1	131.40	0	62.13
1000 m	*V. vulpes*	V02	Slope	1	183.50	0	18.26
	C. lupaster	A04	Distance to isolated houses	1	118.83	0	21.24
	G. genetta	G02	Distance to the nearest pave road	1	59.45	0	56.44
	C. lupus familiaris	C02	People abundance	1	131.40	0	62.13

Table 4
Estimates of beta coefficients and standard error (SE) for covariates contained in the best GLM models. For model codes see Table 3.

Model	Intercept	Slope	Proportion of dense forest	Altitude	Distance to isolated houses	Distance to the nearest pave road	People abundance
V01	−14.6718 (7.9365)	1.535 (0.3457)					
A01	−33.9716 (18.4681)		0.0287 (0.026)	0.0241 (0.013)			
A02	−40.848 (17.4702)			0.0295 (0.012)			
A03	−1.9501 (2.0596)		0.0271 (0.028)		0.0035 (0.0023)		
G01	−0.3756 (0.2854)					0.0011 (0.0002)	
C01	1.2763 (1.427)						0.7981 (0.437)
V02	−10.961 (14.677)	2.0246 (0.0982)					
A04	−1.7017 (2.039)				0.0461 (0.0356)		
G02	−0.3756 (0.2854)					0.0011 (0.0002)	
C02	1.2763 (1.428)						0.7981 (0.1437)

dog, its presence in the sampled area was clearly related to the abundance of people (Table 3), explaining this variable more than 50 % of the variance of the data in the model. As in the previous species models, the abundance of people presented a positive influence for this species.

The GLMs did not detect significant effects of the variable that characterized the protection of the area. However, we found striking differences in some species' abundance between the protected area and the non-protected area (Fig. 2), as it happens with foxes and hares.

4.3. Spatial overlap

The domestic dogs had a positive association with genets (φ = 1,37) and a negative association with red foxes (φ = 0,89). Red foxes and genets were negatively associated (φ = 0,91), while φ values for the other species dyads were close to 1, indicating no association (φ = 0,97−−1,05, Fig. 3).

4.4. Temporary overlap

The carnivore species differed in their daily activity patterns. *Canis lupaster* had early morning habits, while the *Vulpes vulpes* were mostly nocturnal. Red foxes showed an increase of its activity when the wild dominant species were less active. Even so, they overlapped their activity patterns (Fig. 4). *Canis lupus familiaris* had a marked diurnal activity that coincide with absence periods of African golden wolves and red foxes. Overlap rates were very low between domestic dogs and these two other species, indicating that they hardly ever interact (Fig. 4). Regarding *Genetta genetta*, they were more active when African golden wolves and red foxes were not present, having also low overlap rates with both species.

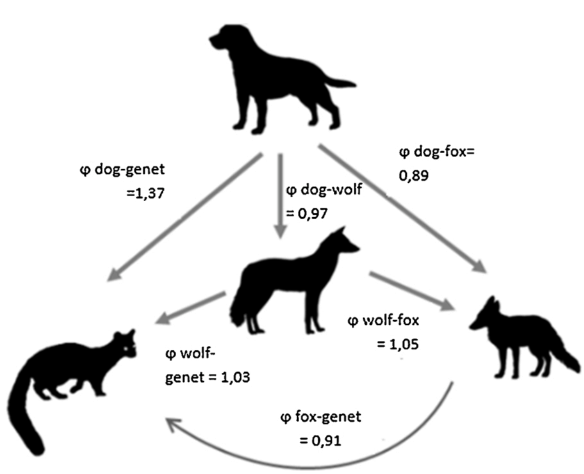

Fig. 3. Dominance relations and interaction factor (φ) of the carnivore species of the Middle Atlas community. The arrowhead indicates the subrogated species.

There was a great overlap between the activity of *Vulpes vulpes* and the micromammals, showing similar activity patterns (Fig. 5). Genets overlapped much less with the micromammals (Fig. 5). Moreover, a high rate of overlap was also found between hares and red foxes, but this overlap was much lower with African golden wolf (Fig. 5).

5. Discussion

5.1. Habitat selection patterns

The interspecific differences shown in habitat selection highlights the choice of different hunting or resting places as one important behavioural mechanism that favours coexistence in carnivores (Hearn et al., 2018), reducing the competition between them. The African golden wolf selected different environmental variables according to buffer size, which underlines the role of scale in the study of habitat selection (Martín-Díaz et al., 2018). It seems that vegetation, topography and degree of humanization influenced in African golden wolf habitat selection at a micro-scale level. This species was more abundant or used with greater intensity those places where the dense forest was well conserved. In this scenery, the African golden wolf will find its prey more easily (Eddine et al., 2017) without having to travel very far, and also constitutes a good area to find a refuge. Altitude and distance to isolated houses also positively influenced the relative abundance of the species, which seems to suggest that the avoidance of humans is a key factor to survive. This behaviour is typical in rural areas, where livestock predation leads to intense persecution of African golden wolves by locals (Schumann et al., 2012). At a larger scale (1000 m buffer radius), these animals chose again places far from human settlements, so it seems that the human-carnivore conflict is a significant pressure in this area.

The positive effect of the slope on the presence of the red fox may indicate the selection of areas with difficult access for humans, as it has been documented for other species in places with anthropogenic influence (Jiménez et al., 2017; Martín-Díaz et al., 2018). These results contradict most studies conducted in fox ecology, which classify this species as generalist in terms of habitat selection (White et al., 2006; Sarmento et al., 2011). The use of occupancy models instead of RAI is likely to lead to such deductions (Goldyn et al., 2003; Jiménez et al., 2017). As it is shown in our study, although foxes were present in most of the territory (Table 2), they were more abundant in certain areas or used them more intensively.

The model results for the genet indicated that its abundance is related to the distance to the road, for both buffer sizes. The species may be avoiding the main roads because they are a cause of high mortality or because noise may compromise their daily activities (Grilo et al., 2009). However, given the small number of records obtained, the results should be taken with caution, as they may not correctly reflect the habitat

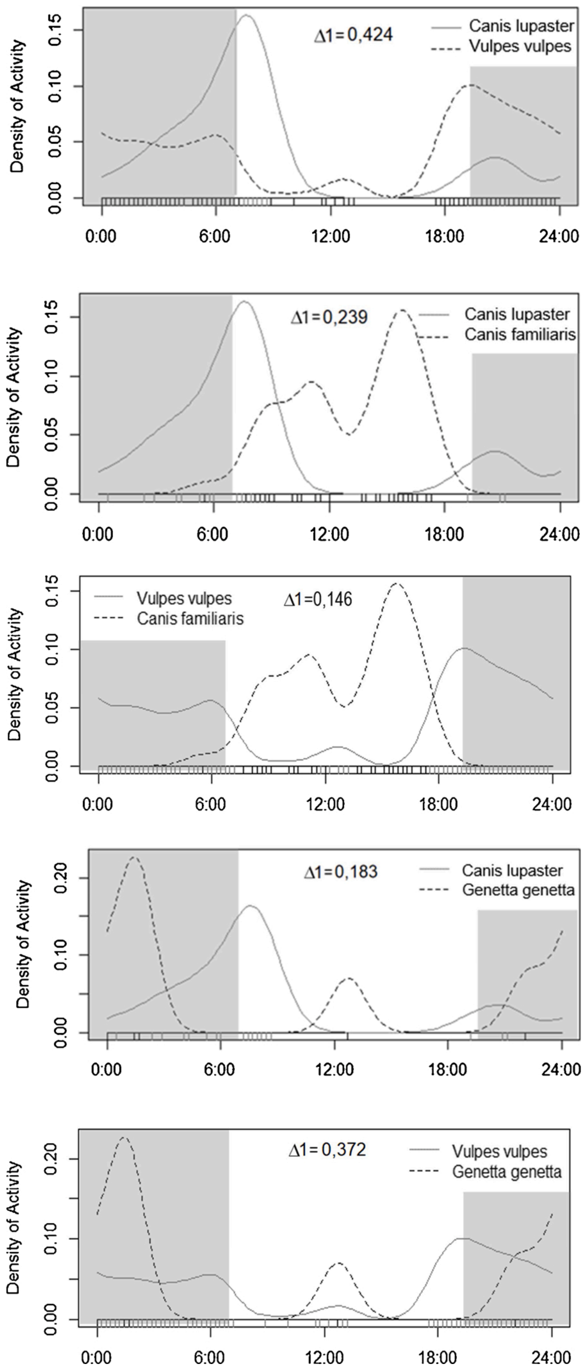

Fig. 4. Overlapping of daily activity patterns between dyads of carnivores. The overlap coefficient is shown in the centre of the graphic. The shaded area indicates the twilight period.

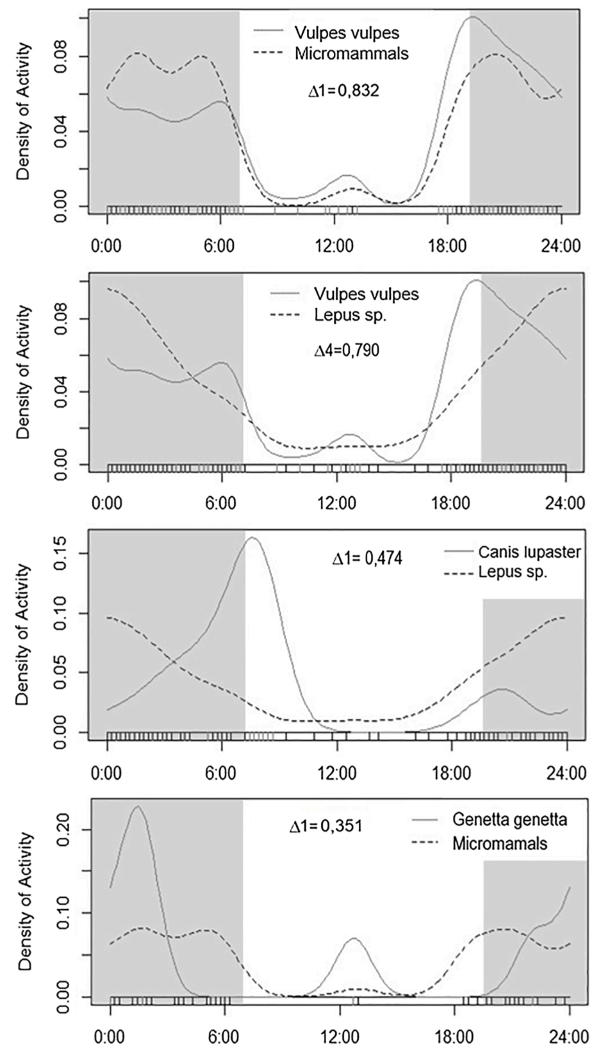

Fig. 5. Overlapping activity patterns between some carnivores and their prey. The overlap coefficient is shown in the middle of the graphics. The shaded area indicates the twilight period.

selection patterns of the species as a whole (Mackenzie and Nichols, 2004). The abundance of the domestic dog was clearly linked to the abundance of people. As carnivores find on the livestock a quick and easy way to obtain food, domestic dogs are usually used to dissuade them (Schumann et al., 2012). If the results are examined carefully, it can be shown that most of the habitat selection variables were related to anthropic factors; for example, African golden wolves selected high places away from houses, red foxes preferred steep slopes to reduce encounters with humans and genets avoided the main roads. It follows, therefore, that human influence is the prime factor, probably constituting a severe selective pressure for the survival of the sampled species.

It was also expected that the small protected area would have a greater impact on the presence and abundance of carnivores. Being an area in which any type of human exploitation is prohibited, including grazing, it gives an opportunity to hares and micromammals to expand within the area, which should lead to a greater presence of carnivores (Pyke et al., 1977; Begon et al., 2006). However, our results did not show any effect of this small protected area on the carnivore abundance (Fig. 2). As we could see on the data collection, there were some captures of shepherds with their livestock passing by, so it could indicate that the measurements taken by the government are not as strict as we thought. Another reason for these results could be that the size of the protected area is not big enough to have consequences on carnivores' populations, as it happens in other protected areas (Mitchell and Hebblewhite, 2012). Even so, some interesting trends could be highlighted. The African golden wolf was the only carnivore that presented an apparent greater abundance within the protected area related to the surrounding area, while the other carnivores were less abundant or absent, which could be due to competitive exclusion (Vanak et al., 2013; Ripple et al., 2014). These apparent tendencies show us the importance of having more detailed studies about this matter, in which the increase in sample size may be a key element to achieve the statistical significance level.

5.2. Spatial overlap

One of the mechanisms that allows carnivores to coexist is the spatial segregation, decreasing interspecific competition (Vanak et al., 2013). In our study, most of the values obtained from the spatial overlap index (φ) were very close to 1, indicating that the spatial distributions are mostly independent (Mackenzie et al., 2006). That is seen, for example, between African golden wolves and domestic dogs, red foxes or genets. This means that other avoidance mechanisms, as temporal segregation, could be more important for their distributions. The exclusion between domestic dogs and red foxes was expected as red foxes could have developed spatial avoidance mechanisms in the face of the aggressive persecution by farmers and their dogs in rural areas (Gusset et al., 2009; Schuette et al., 2013). The spatial association presented by domestic dogs with genets could be explained by the fact that they do not share the same niche or habits. Also, the presence of domestic dogs can help to reduce an important competitor of the genet, the red fox (Carvalho and Gomes, 2001). Red foxes and genets found on the spatial segregation an efficient mechanism to reduce the exploitative competition between them, due to the highly overlap of their trophic niches (Ferreras et al., 2016),

5.3. Temporal overlap

Temporal segregation of activities minimizes interspecific competition by reducing the likelihood of direct encounters between dominant members of the community, who govern the time zone that suits them best, and the subordinate ones, who tend to shift their periods of activity to coexist (Carvalho and Gomes, 2001; Sarmento et al., 2011). In our carnivore community, foxes and genets showed temporal patterns that tend to avoid those periods when the African golden wolf is more active. It seems then that temporal avoidance is a strong mechanism that allows the coexistence of these species, as it happens in other ecosystems (Ferreras et al., 2016; Hearn et al., 2018)

The combined kernel density graphs between the red fox and the African golden wolf regarding the dog, showed a striking temporal segregation. In Middle Atlas, the Barbary dogs are trained and encouraged by the shepherds to chase and kill wildlife, especially with African golden wolves, which are considered as dangerous animals that need to be controlled (Waters et al., 2018). Given the close relationship of humans and dogs, it can be deduced that the detection time of the dog coincide with the period of maximum human activity, dedicated mainly to herding. Thus, a decrease in the activity of these two species in this period will favour their survival, by reducing the possibilities of human-carnivore encounters (Gusset et al., 2009; Schuette et al., 2013).

Carnivores are also highly dependent on their prey to obtain the energy needed to carry out their daily activities. According to the theory of optimal foraging (Pyke et al., 1977), species look for ways to obtain food quickly and at the lowest possible energy cost. Carnivores are capable of achieving this objective by tracking the hours of greatest activity of their prey and adjusting to them (Monterroso et al., 2013; Martín-Díaz et al., 2018). Therefore, it can be expected that the daily activity patterns of this community are also influenced by the presence and abundance of its main prey. Our results revealed a great synchrony between red foxes and micromammals' activity, their main prey in this area (Fig. 5). Their specialization in capturing micromammals (Goldyn et al., 2003; Dell'Arte et al., 2007) is such that their pattern was an almost a copy of that presented by the micromammals. However, the maximum activity peaks of the micromammals were somewhat displaced compared to those of the red fox, avoiding a complete overlap (hypothesis of detection of predation risk; Lima and Bednekoff, 1999). The common genet is considered to have a facultative specialist strategy (Virgós et al., 1999) and field studies in Mediterranean basin from northern Africa also showed micromammals as their main prey (Amroun et al., 2014). Nevertheless, the rate of overlap of the genet with micromammals was much lower, a fact that could be related to a mechanism of temporary avoidance of the genet against the fox, its main competitor (Carvalho and Gomes, 2001).

A certain asynchrony was observed between the activity of African golden wolves and hares. In this area, the hare was the most abundant potential prey, so the low temporal overlap could be explained by their high accessibility to this resource (Monterroso et al., 2013). The African golden wolf is an opportunistic species, which varies its diet depending on the availability of resources (Eddine et al., 2017). In this sense, the hare is only part of the African golden wolf's diet when its main prey, generally medium-sized herbivores, are scarce. In this way, the African golden wolf could be taking advantage of the abundance of hare in the study area to feed on it, even if it does not constitute its main prey.

6. Conclusions

This study shows for the first time the composition and the spatio-temporal ecology of a carnivore community in North-western Africa. Spatial segregation had a marginal role in specie's coexistence in our study areas of the Middle Atlas; nevertheless, human presence must be taken into account, as it severely affected the carnivore's behaviour. In this sense, it is important to highlight the need to study in depth the wildlife communities of North Africa in order to create adequate conservation plans and also to increase the effectiveness of protected areas. Although, unfortunately, it is too late for some emblematic species, such as the Barbary leopard, there is still a chance for the rest of the species, including not only the recently described African golden wolf but for the extremely rare North African caracal.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.zool.2021.125904.

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