# Determinants of seasonal variation in activity patterns of mouflon

**G. Bourgoin, M. Garel, B. Van Moorter, D. Dubray, D. Maillard, E. Marty, and J.-M. Gaillard**

**Abstract:** Balancing energetic requirements is a complex process governed by the current condition of the animal, its physiological state, and by the local environment. In response to these factors, animals are expected to adapt their activity patterns. Based on continuous monitoring of 14 GPS-collared animals in southern France, we studied how environmental conditions and reproductive life-cycle periods shape the monthly activity patterns of free-ranging female mouflon (*Ovis gmelini musimon* × *Ovis* sp. (Blyth, 1841)). More specifically, we analyzed total daily activity, diurnal activity, length of activity bouts, and number of activity bouts. We performed multivariate analyses to account for the relationship between several intercorrelated explanatory variables and monthly activity variables. Mouflon decreased their daily activity, diurnal activity, and length of activity bouts during the hot summer months. Such changes might allow animals to reduce thermo-regulation costs. The resulting higher activity in winter compared with summer indicates that summer is the most limiting period for large herbivores in Mediterranean area. Both the number of active bouts and the daily activity increased during spring, when females have access to increased food quality, which ensures a faster digestion, and when they may face high energetic requirements owing to reproduction.

**Résumé :** Couvrir ses besoins énergétiques est un processus complexe qui varie en fonction des conditions actuelles de l'animal, de son statut physiologique et de l'environnement local. En réponse à ces facteurs, les animaux sont supposés adapter leur rythme d'activité. À partir d'un suivi continu de 14 animaux équipés de colliers GPS dans le sud de la France, nous avons étudié comment les conditions environnementales et les périodes du cycle de reproduction modifiaient le rythme d'activité mensuel de femelles de mouflon (*Ovis gmelini musimon* × *Ovis* sp. (Blyth, 1841)) en nature. Plus spéci-fiquement, nous avons analysé l'activité journalière, l'activité diurne, la durée des phases d'activité et le nombre quotidien de phases d'activité. Nous avons utilisé des analyses multivariées afin de prendre en compte les relations entre les nombreuses variables explicatives co-linéaires et les variables d'activité mensuelle. Les mouflons diminuent leur activité jour-nalière, leur activité diurne et la durée des phases d'activité durant les mois chauds de l'été. De tels changements devraient permettre aux animaux de réduire les coûts de la thermorégulation. La plus forte activité observée en hiver par rapport à l'été indique que l'été est la période la plus limitante pour les grands herbivores vivant en zone méditerranéenne. Le nombre de périodes d'activité ainsi que l'activité journalière augmentent durant le printemps lorsque les femelles ont accès à une alimentation de meilleure qualité permettant une digestion plus rapide, et lorsqu'elles doivent faire face aux besoins énergétiques élevés engendrés par la reproduction.

## Introduction

Optimal foraging theory (OFT; Charnov 1976; Stephens and Krebs 1986) predicts the foraging tactic an animal should adopt to maximize its energy acquisition per unit of foraging time. According to Stephens and Krebs (1986), environmental conditions (e.g., climatic conditions, forage abundance and quality, population density, and human disturbance), and the physiological state and condition (e.g.,

gut fill volume, reproductive status, hormonal state, and body reserves) of animals are the main constraints for such an optimization.

Adverse climatic conditions increase the risk of hyper- or hypo-thermia for ruminants. Ruminants generate heat from metabolism, muscular activity (locomotion, mastication, di-gestive motility), and rumen fermentation (Silanikove 2000; Morand-Fehr and Doreau 2001). As homeotherms, they are expected to adapt their behavior and physiological state to

**G. Bourgoin and M. Garel.** Université de Lyon, université Lyon 1, Centre National de la Recherche Scientifique (CNRS), Unité Mixte de Recherche (UMR) 5558, Laboratoire de Biométrie et Biologie Evolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69622, France; Office National de la Chasse et de la Faune Sauvage, Centre National d'Étude et de Recherche Appliquée sur la Faune de Montagne, 95 rue Pierre Flourens, B.P. 74267, 34098 Montpellier CEDEX 05, France.
**B. Van Moorter and J.-M. Gaillard.**[1] Université de Lyon, université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69622, France.
**D. Dubray and D. Maillard.** Office National de la Chasse et de la Faune Sauvage, Centre National d'Étude et de Recherche Appliquée sur la Faune de Montagne, 95 rue Pierre Flourens, B.P. 74267, 34098 Montpellier CEDEX 05, France.
**E. Marty.** Office National de la Chasse et de la Faune Sauvage, Délégation Régionale Auvergne-Languedoc-Roussillon, Fagairolles, 34610 Castanet-le-Haut, France.

[1]Corresponding author (e-mail: gaillard@biomserv.univ-lyon1.fr).

maintain a constant body temperature independent of the ambient temperature (Silanikove 2000; Morand-Fehr and Doreau 2001; Cain et al. 2006). When facing adverse climatic conditions (e.g., precipitation, low or high temperatures, and snow cover), ruminants can limit costs of thermoregulation by seeking cover (Mysterud and Østbye 1999), decreasing global activity, and (or) switching activity to more favorable periods (e.g., Beier and McCullough 1990).

Both low food abundance (e.g., plant height and density; Illius and Gordon 1987; McGilloway et al. 1999) and high fiber content (Shipley and Spalinger 1992; Abijaoude et al. 2000) decrease the short-term intake rate of ruminants. Thus, longer feeding bouts are necessary to fill the rumen on sparse vegetation of low quality, whereas low food quality leads also to longer rumination and retention periods, and to lower voluntary food intake (e.g., Burns et al. 1997; Abijaoude et al. 2000). Hence, daily energy intake is limited either by ingestion (i.e., handling and searching for food) or by digestion (i.e., the "rumen fill theory"; Moen 1973; Westoby 1974) depending on food availability or food quality, respectively (Wilmshurst et al. 1999). As climatic conditions control plant abundance and quality, the limitation for an individual's daily intake will likely change between seasons.

In addition to variation of environmental conditions, animals are confronted also with variations of their energetic requirements, notably for females according to their reproductive status. Energetic requirements of reproductive females peak during the late-pregnancy and early-lactation periods (Oftedal 1985; Clutton-Brock 1991), leading to increased daily forage intake (Stanley et al. 1993; Kaske and Groth 1997) and level of activity (Neuhaus and Ruckstuhl 2002; Hamel and Côté 2008) of reproductive females.

Therefore, to meet a long-term positive energy balance, animals should adapt their foraging behavior and activity patterns to their internal state and to the current environmental conditions (Stephens and Krebs 1986; Owen-Smith 1994). Relatively few studies on free-ranging ungulates have been performed to cover both diurnal and nocturnal periods over one complete annual cycle (but see Georgii 1981; Beier and McCullough 1990; Green and Bear 1990). Here, we studied the effects of climatic conditions, vegetation quality, and reproductive life-cycle periods on activity patterns of free-ranging female Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp. (Blyth, 1841)) in southern France. As adverse climatic conditions lead to increased energetic expenditure for thermoregulation, we expected that mouflon decrease their level of activity during the hot Mediterranean summer (hypothesis 1*a*) (Garel et al. 2004) to limit heat stress. Similarly, mouflon were expected to decrease their activity during the hottest daily period in summer (i.e., daytime) (hypothesis 1*b*). During winter, mouflon should decrease their global activity (hypothesis 2*a*), especially during the coldest daily period (i.e., nighttime; hypothesis 2*b*), to limit heat loss. We also expected that forage quality should influence the activity pattern of mouflon with the shortest ruminating bouts when high-quality food is available (i.e., spring) (hypothesis 3).

## Materials and methods

### Study area

The population of mouflon inhabits the Caroux-Espinouse area (43°38′N, 2°58′E) in the southwestern border of the Massif Central, in southern France. Elevation ranges from 150 to 1124 m above sea level. The confluence of three climatic influences (atlantic, mediterranean, and mountain) in this area leads to hot and dry summers (mean (SE) daily temperature = 18 ± 0.2 °C and mean (SE) cumulative precipitation = 105 ± 18 mm in June–August 2003–2005; Météo France weather station of Cambon and Salvergues located at 900 m above sea level), wet autumns (mean (SE) cumulative precipitation = 683 ± 256 mm in September–November 2003–2005) and fairly cold winters (mean (SE) daily temperature = 1.6 ± 0.2 °C in December–February 2003–2006). During winter, snow occurs usually for a few days annually (mean (SE) = 18 ± 1 days in December–April 2003–2006). Forests are composed of European beech (*Fagus sylvatica* L.), European chestnut (*Castanea sativa* P. Mill.), holly oak (*Quercus ilex* L.), and pine (genus *Pinus* L.), whereas open areas are mainly covered by moorlands of heather (*Calluna vulgaris* (L.) Hull), Scotch heath (*Erica cinerea* L.), Provence broom (*Cytisus purgans* (L.) Boiss.), Scotch broom (*Cytisus scorparius* (L.) Link) and mixed with grasses (e.g., east alpine violet fescue (*Festuca paniculata* (L.) Schinz & Thell.), sheep fescue (*Festuca ovina* L.), colonial bentgrass (*Agrostis capillaris* L.)). The study area is devoid of any large predators. For further information on the study area see Garel et al. (2005).

### Female activity

#### Trapping

We trapped 14 females during spring–summer from 2003 to 2005 using either individual traps baited with salt, driving nets, or dart-gunning with a compressed air pump gun using a mixture of two anesthetic agents: xylazine and acepromazine. All the trapped females inhabited the slopes of a plateau; nine of these females were living on the west slope (95% kernel home-range overlap: mean = 43.4%, SD = 32.8%; Worton 1989) and four on the south slope (95% kernel home-range overlap: mean = 49.0%, SD = 35.2%), suggesting that available habitats were roughly similar between females.

#### Motion sensors

We equipped trapped females with Lotek 3300S (revision 2) GPS collars (Lotek Engineering Inc., Newmarket, Ontario, Canada). Movements were recorded using two perpendicular captive-ball tilt switches inside GPS collars. Each motion sensor is composed of a ball inside a cylinder. At each end of the cylinder, a pin registers a count each time the ball contacts it with a maximal count value of 255 for each 5 min period. As motion sensors are on perpendicular axis and parallel to the ground when the collar is vertical, one motion sensor is most sensitive to left–right movements (left–right sensor), whereas the other sensor is most sensitive to forward–backward movements (forward–backward sensor; Lotek Engineering Inc. 2003). The forward–backward sensor also computes the proportion of time an individual is head down (i.e., collar angle with vertical position is higher than 7.5°) for each 5 min period.

#### Calibration

Direct observations of free-ranging females fitted with

GPS collars are difficult in the study area because of irregular topography and mosaic of forested habitats (Garel et al. 2007). We thus calibrated the measure of activity from direct observations of four free-ranging collared (Lotek 3300S) female mouflons in the Parc Naturel Régional des Bauges (Alps, France; 45°40′N, 6°13′E; see Garel et al. 2005). Two of us (G.B. and B.V.M.) recorded the activity of females using a tape recorder and digital clock synchronized on GPS time for 8 days (from 27 June to 13 July 2006). Animals were classified either as inactive when they were lying (i.e., sleeping, ruminating, or resting) or as active (i.e., feeding, standing, travelling, or doing other activities such as interactions or scratching). Only 5 min periods of complete activity or inactivity were used during calibration ($n$ = 586; 84 active periods and 502 inactive periods).

After standardization (i.e., centered and scaled) of the motion sensor data (three movement data types: left–right, forward–backward, and head down; see above) of each focal individual, we performed a linear discriminant analysis (Krzanowski and Marriot 1994) that allowed us to split observations into active vs. inactive classes according to motion-sensor values. We computed the model on a random subsample of the data set (50% of the data) using an equal a priori class membership probability (i.e., $p$ = 0.5). Then, we applied the model on the remaining data (50%) and looked at the proportion of 5 min periods correctly classified as either active or inactive.

Based on 1000 replicates of this procedure, we obtained high success rates with 85.4% (95% confidence interval (CI) = 77.4% and 93.6%) and 87.3% (95% CI = 81.9% and 91.6%) of animals correctly classified as active or inactive, respectively. After the calibration procedure, we used the whole data set ($n$ = 586 periods) to compute a new linear discriminant model. We applied this model to data collected from the 14 free-ranging females studied here, again after standardization of the data from their motion sensors.

## Activity data and explanatory variables

Data were collected from June 2003 to December 2005. For each month of a given year we had activity data from 2 up to 7 females (mean = 5.1, SD = 1.4), and for each female we recorded activity from 5 to 14 months (mean = 10.3, SD = 3.2).

As activity patterns of ruminants consist of a succession of inactive and active bouts, we considered that an activity or inactivity bout began when at least three successive 5 min active or inactive periods occurred. Based on this data set, we computed the mean values for each month of (1) the proportion of time a female was active per day (pA), (2) the proportion of daily activity that occurred per daytime hour (pADt, computed as the time active during daytime / time active during nighttime × daytime duration (h)), (3) the number of active bouts per day (nAB), and (4) the length of active bouts (lAB).

Large mammalian herbivores spend most of their active time feeding (e.g., Moncorps et al. 1997; Shi et al. 2003); therefore, we assumed that the time mouflon spend active should mostly reflect their foraging activity. We used a temporal resolution of 1 month, which is commonly used (e.g., Beier and McCullough 1990). Moreover, some of the explanatory factors we studied were not measured at a temporal scale finer than a month (see below). Hence, we averaged data for each month of each year. Using a linear mixed model with constant term as the fixed effect and female identity as the random effect (Pinheiro and Bates 2000), we computed the observed variability in nAB, lAB, pADt, and pA accounted for by the female identity after log transformation of nAB and lAB and arcsine transformation of pA and pADt.

In this study, we looked for assessing the global pattern of activity. Moreover, we did not measure food quality at the individual scale but rather at the population scale. Hence, we performed our analyses on the activity data of an average individual (i.e., we computed the mean of the activity measures of females for each month of each year).

## Factors of variation in female activity

### Food quality

From June 2003 to December 2005, we collected pellet samples of mouflon (mean = 57.9, SD = 9) twice each month in open areas. We included pellets from both sexes because we could not distinguish between pellets from either sex. However, a previous study in this population did not report any between-sex difference in autumn–winter diet (Cransac et al. 1997). Thus, we assumed that fecal analysis based on pellets from both sexes was representative of the seasonal variation in female diet quality.

Pellets ($n$ = 1800) were dried at 60 °C during 72 h, then ground. We used the near-infrared reflectance spectroscopy (Foley et al. 1998) analysis to assess the chemical composition of pellets. The method consists of measuring the absorption of near-infrared radiation (400–2500 nm) by organic compounds of the sample, which provides information on chemical components of the pellets.

However, a calibration procedure had to be performed first to determine the chemical composition of pellets from the spectral analysis. Therefore, we performed reference chemical analyses on 120 samples to measure their neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (Van Soest et al. 1991), and fecal nitrogen (FN) contents. We regressed these measures on corresponding infrared spectra using polynomial least-squared regressions (Tenenhaus et al. 1995). After this calibration procedure, we applied the model on the spectra of the 1800 samples and computed the monthly mean value for each of the chemical components.

The FN content reflects food quality (Holloway et al. 1981; Hodgman et al. 1996). In contrast, an increase of cell-wall constituents in the diet (expressed by NDF, ADF, and ADL) leads to longer rumination and retention periods and to a decrease in food intake (e.g., Burns et al. 1997; Abijaoude et al. 2000).

### Vegetation growth index

The normalized difference vegetation index (NDVI) allows assessing vegetation phenology at a large spatial scale (Reed et al. 1994). NDVI is derived from the ratio of red to near-infrared reflectance and is known to be strongly correlated with aboveground net primary productivity, leaf area in canopy, and absorbed photosynthetic active radiation (for

reviews see Kerr and Ostrovsky 2003 and Pettorelli et al. 2005).

We used data from SPOT images (spatial resolution: 1 km × 1 km; temporal resolution: 10 days) to assess the variability in vegetation biomass (Saint 1996). We computed NDVI values using the 23 pixels covering the area used by the 14 studied females. We applied a nonlinear running median line-smoother algorithm (Tuckey 1977) as proposed by Reed et al. (1994) on NDVI time series to limit the negative influence of clouds on prediction of field biomass. For each 10 day period, the highest NDVI value of the 23 pixels was retained (see Holben 1986), and then for each month, we computed the sum of the three corresponding values (integrated NDVI, see Reed et al. 1994). The change in INDVI values between months (INDVIdiff) was then computed to estimate the periods of vegetation flush or senescence.

### Climatic conditions

For each month, we took the mean minimum, mean maximum, and mean daily temperatures and the mean wind speed. We also computed the total rainfall that occurred during the month. We obtained climate data from the Météo France weather stations at Cambon-et-Salvergues (temperature and rainfall — elevation: 900 m above sea level; location: 43°37′N, 02°51′E; distance from the study area: 9.9 km) and Fraïsse-Murat (wind speed — elevation: 1041 m; location: 43°38′N, 02°49′E; distance from the study area: 13.2 km).

### Reproductive life-cycle periods of females

We distinguished five life-cycle periods within the year to reflect temporal variation in energetic requirements and metabolic costs of females: (1) "early gestation" from November to January; (2) "late gestation" from February to March; (3) "early lactation" from April to May; (4) "late lactation" in June; (5) "nonreproductive stage" from July to October (Pfeffer 1967; Bon et al. 1993).

All females monitored during the high energetic requirement period (i.e., end-gestation and lactation periods) were adults. Although direct observations of reproductive status were not available, we assumed that most collared females were reproducing because of the high pregnancy rates (0.91 for an adult female; Garel et al. 2005) observed in this population. Thus, the probability that 11 or more females, from the 14 we monitored, effectively gave birth is 0.97.

### Co-inertia analysis

Because of the high number of intercorrelated explanatory variables ($n = 11$) used in our study, we performed a co-inertia analysis (Dolédec and Chessel 1994; Dray et al. 2003). This method provides a measure of the relationships between two data sets, and for each data set many variables can be included in the analysis without restrictive assumptions of independence (Dolédec and Chessel 1994). In addition, relationships between explanatory variables and different measures of the activity pattern can be assessed within the same analysis.

Co-inertia analysis is a multivariate analysis maximizing the co-inertia (i.e., the concordance) between two data arrays. In the first array ("environmental array"), the observations for each month from all years were entered row-wise

and the different environmental variables column-wise. The different columns were measurements of forage quality (FN, NDF, ADF, ADL), vegetation growth index (INDVIdiff), climate (minimum, maximum, and mean daily temperatures; wind speed; cumulative precipitation) and "reproductive life-cycle period" (categorical variable; see above). The rows of the second array ("activity array") contained the observed values for the average female during each month from all years, with column-wise the four activity measurements (pA, pADt, nAB, lAB).

In a first step, we performed separate multivariate analyses of each data array (i.e., the environmental and the activity array) to find the axes maximizing the variability (or inertia) for both arrays. We weighted the activity measures using the number of females included in the computation (between 2 and 7 females per month of a year). We thus gave more weight in the analysis to data with large sample size. From the principal component analysis (PCA) extended to include both discrete and continuous variables (Hill and Smith 1976) and performed on the environmental array (called here PCA1), we retained the two first axes (accounting for 43.7% and 21.1% of the observed variation in environmental data, respectively). From the PCA performed on the activity array (called PCA2), we also retained the two first axes (accounting for 62.8% and 26.0% of the observed variation in activity patterns, respectively).

Then, we performed the co-inertia analysis to find new axes in the PCA1 hyper-volume ("environmental axis") and new axes in the PCA2 hyper-volume ("activity axis") so that the squared covariance between the new projections of the months on the activity axis and on the environmental axis was maximal (for further details on the method see Dray et al. 2003). To test the significance of the resulting correlation (noted $R$ value) between the two new sets of coordinates resulting from the co-inertia analysis, we performed a randomization test (Dolédec and Chessel 1994). After random permutation of the rows from both arrays, a new co-inertia analysis provided a new $R$ value; after replicating this procedure 1000 times, we obtained a distribution of the correlations when the structure between both arrays is random owing to the permutations. We then compared the computed $R$ values from the original data set to this distribution to assess their level of significance.

The most closely linked variables between the two data sets are those having the highest coordinate values on the co-inertia axes. However, the relative importance of categorical vs. continuous variables cannot be addressed. This means that the coordinates of the five classes of the categorical "reproductive life-cycle period" variable (i.e., early gestation, late gestation, early lactation, late lactation, nonreproductive stage) are compared among each other, but not with the coordinates of the quantitative variables (i.e., forage quality (FN, NDF, ADF, ADL), vegetation growth index (INDVIdiff), climatic data (minimum, maximum, and mean daily temperatures; wind speed; cumulative precipitation)).

We performed statistical and co-inertia analyses with R version 2.6.0 (Ihaka and Gentleman 1996) using library "ade4" (Chessel et al. 2004). We computed kernel home-range overlap using the function "kerneloverlap" in the "adehabitat" library (Calenge 2006). We conducted linear discriminant analyses using the function "lda" in the

**Fig. 1.** Mean values of (*a*) the proportion of time active per day (pA), (*b*) the proportion of daily activity occurring during daytime and corrected for daytime duration (pADt, computed as the time active during daytime / time active during nighttime × daytime duration (h)), (*c*) the number of active bouts per day (nAB), and (*d*) the length of active bouts (lAB) of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in year 2003 (open circles), 2004 (shaded circles), and 2005 (solid circles) in Caroux-Espinouse, France. Symbol size is proportional to the number of females used to compute the value (between 2 and 7 females). The broken lines represent the weighted mean activity value computed from the data of all the females.
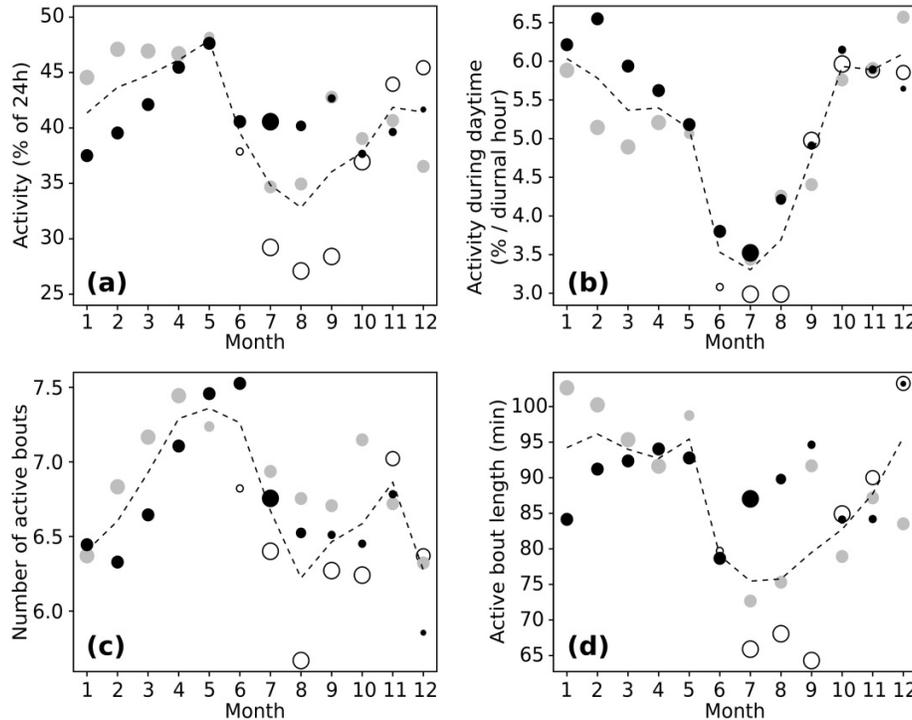


"MASS" library (Venables and Ripley 2002) and linear mixed model using the function "lme" in library "nlme" (Pinheiro and Bates 2000).

## Results

### Activity data

We found that 19.9%, 16.7%, 6.1%, and 3.2% of the observed variability in the number of active bouts (nAB), the length of active bouts (lAB), the proportion of daily activity that occurred during daytime corrected for daytime duration (pADt), and the proportion of time a female was active per day (pA), respectively, was accounted for by the female identity. This indicates that, at least for pADt and pA, female heterogeneity was very low so that most of the variation in activity patterns was caused by differences between months.

The proportion of time a female was active per day (pA) increased from January onwards (41.3%) to reach a peak in May (47.9%; Fig. 1*a*), whereas the proportion of activity during daytime (pADt) slowly decreased during the same period (from 6.0% to 5.1%/diurnal hour; Fig. 1*b*). Together with the increased activity, the number of activity bouts (nAB) increased (from 6.4 to 7.4; Fig. 1*c*) but not their length (lAB; mean = 94.5 min; Fig. 1*d*). A strong decrease of pA and pADt, as well as lAB, occurred in June (Figs. 1*a*, 1*b*, and 1*d*, respectively), and nAB decreased in July (Fig. 1*c*). The lowest values of pA, pADt, and lAB occurred during the summer months (June–August — mean

observed value: 35.7%, 3.5%/diurnal hour, and 76.8 min, respectively; Figs. 1*a*, 1*b*, 1*d*). From September to November, the four measures of activity increased.

### Factors influencing the activity of females

The overall similarity in the structure of the environmental data set and the activity data set highlighted by the co-inertia analysis resulted in a RV coefficient (i.e., multivariate equivalent of $r^2$; see Robert and Escoufier 1976) of 0.49. Most of this co-structure between the two data sets was accounted for by the first (83.5%) and second (15.1%) axes of the co-inertia analysis (Fig. 2*c*). On the two co-inertia axes, high correlations occurred between the new projection coordinates of the months of the activity and the environmental data sets ($R$ = 0.84 and 0.59; randomization tests: $p < 0.001$ and $p = 0.03$, respectively).

The first environmental axis of the co-inertia analysis corresponded mostly to a thermal gradient and contrasted the hot and dry summer season (from June to August) to the cool, windy, and wet winter season (from November to March; Figs. 2*a*, 2*b*). The second environmental axis of the co-inertia analysis clearly separated the growing season (from April to June; called spring in the following) from the rest of the year (Figs. 2*a*, 2*b*). During spring, the flush of the vegetation occurred (high INDVIdiff values), leading to a rich diet (i.e., high nitrogen content (FN) and low cell-wall content) that reached a peak in May. As lambing and lactation periods occur in spring, the second environmental axis of the co-inertia analysis separated also the lactation pe-

**Fig. 2.** Projection of (*a*) the months, (*b*) environmental variables, and (*d*) activity data from female mouflons (*Ovis gmelini musimon* × *Ovis* sp.) on the first (horizontal) and second (vertical) co-inertia axes of the co-inertia plane. (*c*) Representation of the proportion of co-inertia explained by each of the four axes. Months are numbered from 1 for January to 12 for December. ADF, acid detergent fiber; ADL, acid detergent lignin; FN, fecal nitrogen; INDVIdiff, difference of integrated NDVI with the previous month; lAB, the length of active bouts; maxT, maximum temperature; meanT, mean temperature; minT, minimum temperature; nAB, number of active bouts; NDF, neutral detergent fiber; pA, proportion of time active per day; pADt, proportion of daily activity occurring during daytime and corrected for daytime duration; RLC, reproductive life-cycle period. See text for more details.
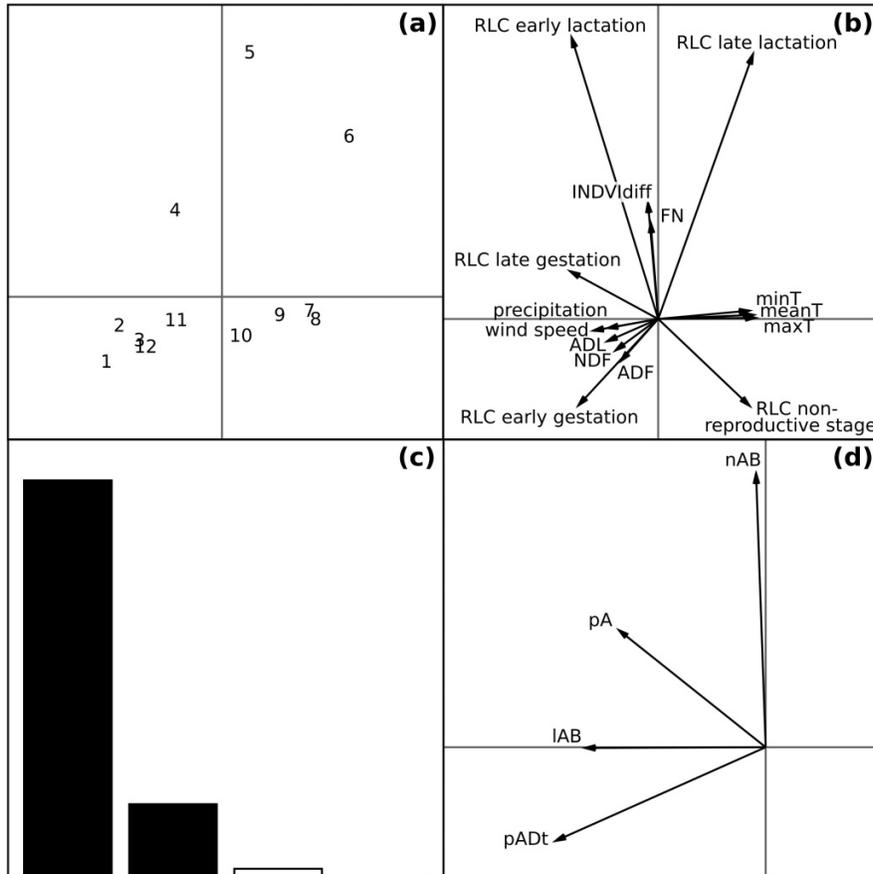


riod from the nonreproductive and early-gestation period (Fig. 2*b*).

The first activity axis of the co-inertia analysis represented mainly the length of active bouts (lAB) and the proportion of daily activity during daytime (pADt), whereas the second activity axis of the co-inertia analysis was highly associated with the variation in the number of active bouts (nAB; Fig. 2*d*). The proportion of time a female was active per day (pA) contributed to both axes of the co-inertia analysis.

Most of the co-structure between the environmental data set and the activity data set (83.5%; Fig. 2*c*) involved relationships among the length of active bouts (lAB), the proportion of daily activity during daytime corrected for daytime duration (pADt), the proportion of time a female was active (pA), and thermal variations (Figs. 2*b*, 2*d*). The lowest values of lAB, pADt, and pA occurred during summer (from June to September; Figs. 2*a*, 2*b*, 2*d*), while the highest values occurred during winter (from November to March; Figs. 2*a*, 2*b*, 2*d*). Most of the variations in nAB, and to some extent variations in pA, were associated with changes in vegetation quality and the reproductive life-cycle

period. The proportion of time a female was active per day and nAB were both highest during spring (i.e., high-quality food and lactation period; Figs. 2*a*, 2*b*, 2*d*).

## Discussion

We tested hypotheses on the factors influencing the activity pattern of 14 free-ranging female mouflons inhabiting Caroux-Espinouse. Our data set allowed us to draw reliable inference on the monthly variations of the daily activity and the proportion of activity during daytime. However, the between-individual variability in the length and the number of active bouts suggest that results should be confirmed with a larger number of females in the data set.

Co-inertia analysis is a suitable multivariate method to search for symmetric patterns between two data sets. This analysis can be performed when a large number of variables are used in each data set, with respect to sample sizes, and when these variables are correlated. Furthermore, co-inertia enables the exploration of relationships between any standard multivariate analyses (e.g., principal component analysis, correspondence analysis, multiple correspondence

analysis) dealing with quantitative and (or) qualitative variables and performed on the data sets (Dolédec and Chessel 1994; Dray et al. 2003).

Reduced dry-matter intake (Silanikove 1992), shorter feeding bouts (Hayasaka 1997), less global activity (Belovsky and Slade 1986; Beier and McCullough 1990; Owen-Smith 1998), and more nocturnal activity (Beier and McCullough 1990; Maloney et al. 2005) have been observed when ungulates experience heat stress owing to high temperatures. These responses facilitate thermoregulation by lowering the heat generated from rumen fermentation, muscular activity (locomotion, mastication, digestive motility), and metabolism (Silanikove 2000; Morand-Fehr and Doreau 2001). Hence, the marked decrease of global activity, bout length, and the switch towards nocturnal activity observed during summer (in support of hypotheses 1a and 1b) clearly demonstrate the negative influence of heat on female activity (particularly during the hot summer of 2003: mean (SE) daily temperature = 20 ± 0.2 °C; Figs. 1a, 1d, 1b).

We similarly predicted a negative influence of winter conditions on activity of mouflon (hypothesis 2a). However, we observed a higher level of activity in winter than in summer (42.6% vs. 35.7%, respectively; Fig. 1a), suggesting that summer climatic conditions (high temperatures, low wind speed, and little precipitation) were more constraining than winter climatic conditions (fairly cold temperatures, high wind speed, and heavy precipitation) in our study area (in support of hypotheses 1a and 1b rather than hypothesis 2a). Only few studies of northern ungulates have previously reported higher activity levels in winter than in summer (Clutton-Brock et al. 1982; Pépin et al. 2006). Most previous studies have been performed in northern areas and reported opposite results with highest activity in spring–summer (e.g., Beier and McCullough 1990; Loe et al. 2007). Such a discrepancy is most likely accounted for by the mediterranean conditions encountered here (high temperatures and low precipitation), the thermal gradient being the most important driver of activity of females (Fig. 2b).

In agreement with hypothesis 2b, mouflon seasonally changed the distribution of their activity between day and night for energy conservation (e.g., Beier and McCullough 1990). They responded to the winter climatic conditions by being more active during the warmer period of the day (i.e., daytime) in winter, while the reverse was observed in summer (proportion of daily activity during daytime corrected for daytime duration: 5.8%/diurnal hour in winter vs. 3.5%/diurnal hour in summer; Fig. 1b).

During spring, we observed an increase in activity and in the number of feeding bouts while the length of active bouts remained roughly constant (Figs. 1a, 1c, 2b, 2d). Hence, mouflon had their shortest resting period during the season of high-quality food as expected in hypothesis 3. A mechanistic explanation is that the high-quality spring food leads to a higher passage rate of the digesta through the digestive tract (e.g., Burns et al. 1997; Abijaoude et al. 2000), allowing ruminants to resume feeding sooner.

Our study allowed the determination of factors influencing the activity pattern of an average female mouflon at the monthly scale. However, further analyses will be required to refine mechanisms involved in the variations of activity pattern. For that, future analyses should then be performed at the individual level and at a finer temporal scale such as a daily scale.

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