

Daily responses of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) activity to summer climatic conditions

G. Bourgoïn, M. Garel, P. Blanchard, D. Dubray, D. Maillard, and J.-M. Gaillard

Abstract: Investigating the factors shaping the activity of large herbivores is of prime importance because changes in their activity patterns may indicate physiological stress, which can affect reproduction and survival of individuals, and thereby population growth. Although climatic conditions are known to impact the activity patterns of large herbivores, few studies have investigated this relationship at a fine temporal scale. From a continuous monitoring of activity, we assessed the influence of temperature and wind on the summer activity of female mouflon (*Ovis gmelini musimon* Pallas, 1811 × *Ovis* sp.) facing summer droughts. Females showed a marked bimodal activity pattern, with activity peaks occurring after dawn and before dusk. When temperature increased and wind speed decreased, the morning activity peak occurred earlier, while the evening activity peak was delayed. Hence, under stressing climatic conditions, female mouflon decreased their diurnal activity while increasing their nocturnal activity. However, this nocturnal increase did not prevent the activity rate over 24 h to decrease during hot nonwindy days compared with cool windy days. Although the occurrence of wind mitigated the negative influence of heat on the diurnal activity, wind had no effect at the daily scale. These findings emphasize the importance of working at different temporal scales when assessing the activity patterns of free-ranging vertebrates.

Résumé : Il est important d'étudier les facteurs influençant l'activité des grands herbivores car les modifications de leurs patrons d'activité peuvent révéler un stress physiologique pouvant affecter la reproduction et la survie des individus, et donc la croissance de la population. Bien qu'il soit reconnu que les conditions climatiques influencent les patrons d'activité des grands herbivores, peu d'études ont été réalisées sur des données à fine échelle temporelle. A partir d'un suivi continu de l'activité, nous avons évalué l'influence de la température et du vent sur l'activité estivale de femelles de mouflon (*Ovis gmelini musimon* Pallas, 1811 × *Ovis* sp.) confrontées à des étés secs. Les femelles présentent un patron d'activité bimodal marqué avec des pics d'activité après l'aube et avant le crépuscule. Lorsque les températures augmentent et que la vitesse du vent diminue, le pic d'activité du matin a lieu plus tôt tandis que celui du soir a lieu plus tardivement. Ainsi, lors de conditions climatiques stressantes, les femelles de mouflons diminuent leur activité diurne tandis qu'elles augmentent leur activité nocturne. Cependant, cette augmentation de l'activité nocturne n'empêche pas une diminution de l'activité sur 24 h durant les jours chauds et sans vent par rapport aux jours plus frais et venté. Bien que la présence de vent tende à limiter l'influence négative de la chaleur sur l'activité diurne, le vent n'a pas d'effet à l'échelle de la journée. Ces résultats démontrent l'importance de travailler à différentes échelles temporelles lors d'études des patrons d'activité des vertébrés sauvages.

Introduction

Along with changes in population density, climatic variations shape the environmental conditions that influence population dynamics of large herbivores (Sæther 1997). Lots of studies have previously reported climatic effects on several life-history traits (for reviews see Gaillard et al. 2000 and Weladji et al. 2002). It has also become clear that environmental variations during individuals' early development can also have delayed long-term effects on their survival and re-

productive performance (cohort effects; red deer (*Cervus elaphus* L., 1758): Albon et al. 1987; mountain goats (*Oreamnos americanus* (Blainville, 1816)), bighorn sheep (*Ovis canadensis* Shaw, 1804), and European roe deer (*Capreolus capreolus* (L., 1758)): Hamel et al. 2009; roe deer: Gaillard et al. 2003). Heat stress can be highly constraining for domestic ungulates, affecting their productivity (e.g., milk production and body growth rate: West 2003; Marai et al. 2007), survival (e.g., Stull et al. 2008), and reproductive abilities (e.g., fertility: Thatcher 1974). Hence, particular at-

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tention should be given to the influence of summer climatic conditions on animals, as it is predicted in the current context of global warming that they will face more intense and frequent heat waves (Paeth and Hense 2005; Déqué 2007).

As homeotherms, ungulates should adapt their physiology and behavior to the environmental thermal conditions to maintain their body temperature within narrow limits. Among their responses, we observed reductions in muscular activity (e.g., travelling, chewing) and intake rate under heat stress, as muscular contractions and rumen fermentation are heat productive (Silanikove 2000; Morand-Fehr and Doreau 2001). Heat stress should thus have a marked effect on their overall activity pattern. Hence, focusing on the variations of their activity pattern in response to climatic variations should allow one to study their response to heat.

In a previous study (Bourgoin et al. 2008), we assessed the factors influencing the mean monthly activity pattern of female mouflon (*Ovis gmelini musimon* Pallas, 1811 × *Ovis* sp.) inhabiting a Mediterranean area. We showed that hot and dry summers constrained mean daily activity and day to night activity ratio, as well as the mean length of the active periods, suggesting that heat stress occurred in some summers. However, refining our understanding of mechanisms involved in the variation of activity patterns requires a finer temporal scale focus.

By using 5 min continuous recording of activity, we assessed the combined effects of temperature and wind during the driest hot month (July) on the hourly activity patterns of female mouflon. We expected mouflon to exhibit a persistent bimodal activity pattern with periods of intense activity that coincide with dawn and dusk despite variation in climatic conditions (H1; Langbein et al. 1997; Pipia et al. 2008). However, we expected mouflon to stop earlier in the morning and to start later in the evening their periods of intense activity during hot days compared with cool days (H2a). We also expected a negative influence of the ambient temperature on the activity of female mouflon during the hottest period of the diurnal period (i.e., midday) to limit the costs of thermoregulation (H2b). Expected decreases of the morning, midday, and evening activity levels may lead to lower diurnal activity (H2c). After a period of restricted access to food resources, ruminants may compensate for the energy deficit by increasing their foraging activity (Iason et al. 1999). Temperature variation within a day (e.g., daytime vs. nighttime) may provide animals with the opportunity to counteract the periods of restricted activity owing to heat with periods of higher activity at lower temperatures. We thus expected the daytime and nighttime activities to be negatively correlated, with an increasing nighttime activity following a hot diurnal period (H2d).

In our study site, wind is a major climatic component (Thiebaut 1971). Although it has been poorly investigated in free-ranging ungulates (white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)): Beier and McCullough 1990; reindeer (*Rangifer tarandus* (L., 1758)): Loe et al. 2007), wind strength, by increasing heat loss (Silanikove 2000; Cain et al. 2006), is expected to improve the thermal balance of ruminants during hot days. We expected female mouflon to stop later in the morning and to start earlier in the evening their periods of intense activity (H3a), and to be more active during the hottest period of the day (i.e., daytime, and more

specifically, midday; H3b) during windy days compared with nonwindy days. We thus expected an increased daytime level of activity under windy conditions compared with nonwindy conditions (H3c), while the nighttime level of activity decreased (H3d).

Materials and methods

Study area

The population of mouflon inhabits the Caroux–Espinouse area (43°38'N, 2°58'E; elevation 150–1124 m above sea level (asl)) in the southern border of the Massif Central, in southern France (for further details see Garel et al. 2005). It is situated at the confluence of three climatic influences: atlantic, Mediterranean, and mountain. The weather conditions are then characterized by hot and dry summers, which negatively influence animal performance (Garel et al. 2004), wet autumns, and fairly cold winters. Wind is common throughout the whole year (139 and 133 days with a mean wind speed >6 m/s in 2004 and 2006, respectively). We trapped and marked mouflon on the Caroux plateau (1050 m asl; southern part of the Massif), where they are faced with hunting from 1 September to the end of February and with hiking all year-round (Martinetto et al. 1998).

Activity data

We used data collected from 17 Lotek 3300S (revision 2) global positioning system (GPS) collars (Lotek Engineering Inc., Carp, Ontario, Canada) with activity sensors fitted on 16 adult females during the springs of 2003–2006 (i.e., one female was trapped and equipped in both 2003 and 2004). Two perpendicular captive-ball tilt (X and Y motion sensors) switches inside GPS collars recorded motions for each 5 min period (values ranging from 0 (no movement) to 255 (highly active)). The Y motion sensor also computed the proportion of time the animal was head down for each 5 min period. Motion data were recorded during 1 ($n = 7$ females), 2 ($n = 8$), or 3 ($n = 1$) successive July months during 2003–2007 (including the severe heat wave in the summer of 2003; Garel et al. 2004).

Exploration of the motion data highlighted a large number of similar high values (≥ 128 counts/5 min period) recorded by the Y sensor of some collars, indicating active animals, whereas the two other motion values (X and proportion head down) recorded low values, suggesting inactive animals (see Kozakai et al. 2008). Because we had no way to discriminate true high Y-sensor values from sensor errors, we replaced each of the Y values ≥ 128 by the mean of the corresponding two surrounding Y values (i.e., Y values recorded during the previous and the following 5 min periods).

In a previous study, we developed a calibration model based on field observations of the activity of free-ranging mouflon fitted with GPS collars (Bourgoin et al. 2008). This calibration model allowed us to predict whether a mouflon was active (i.e., feeding, standing, travelling, or engaged in some other activities such as interacting with conspecifics) or inactive (i.e., lying, ruminating, or resting) for each 5 min period according to the three motion values recorded by its GPS collar (for more details see Bourgoin et al. 2008). Here, we corrected field-observation data sets for the high values of Y (i.e., ≥ 128 counts/5 min period; see above) and computed

a new calibration model that slightly improved the predictive performance of our previous model (Bourgoin et al. 2008): 88.6% (95% confidence interval (CI) = 79.1%–97.2%) and 90.2% (95% CI = 84.4%–94.5%) of animals were correctly classified as active or inactive, respectively (vs. 85.4% (95% CI = 77.4%–93.6%) and 87.3% (95% CI = 81.9%–91.6%), respectively, in the previous model; Bourgoin et al. 2008).

We used this improved calibration model on data recorded from the 17 GPS to predict whether a female was active or not for each 5 min period. We thus computed the proportion of time active (pA) per hour (hourly pA) for each female using the data from the 30 min periods surrounding each hour (e.g., pA at 1400 was computed as the proportion of time active from 1330 to 1430).

Climatic data and ephemerides

We used temperature and wind speed recorded by Météo-France on an hourly basis at 10 m above the ground at the closest weather station to our study area (Météo-France, Fraïsse-Murat; elevation 1041 m asl, 13 km away from the study area). This weather station shared similar environmental conditions with our study area. We used remote climatic conditions as a proxy of the microclimate experienced by the animal. Accordingly, we found strong correlations between the temperature recorded at the weather station and the ones recorded by the thermal sensor of the GPS (mean $R = 0.83$, $SD = 0.04$). Because the GPS collars did not record the wind speed and were themselves proxies of the local temperature (thermal sensor was influenced, for instance, by the behavior of the animal and its body position, i.e., resting vs. standing), we only used data recorded at the weather station. Mean daily temperature and wind speed in July of 2003–2007 were 17.3 °C (10% quantile = 12.1 °C; 90% quantile = 22.1 °C) and 5.0 m/s (10% quantile = 2.4 m/s; 90% quantile = 7.9 m/s), respectively.

We used the civil twilight definition (sun 6° below the horizon) to discriminate between day and night periods. As mean twilight in July occurred at 0347 and 2000 UTC, we defined day and night periods as the 0400–2000 and 2100–0300 UTC time periods, respectively. Midday was defined as the 0800–1600 UTC time period (i.e., a period of half the duration of the day period and roughly centered between dawn and dusk).

Statistical analyses

We used generalized linear mixed models (GLMM) with binomial error and logit link to investigate the influence of temperature and wind speed on the proportion of time a female was active per hour. We expected the observations to be correlated within each female-year and therefore used mixed models including this structure as a random effect. To get independent predictors, we accounted for the effect of wind speed on temperature by using residuals of the regression of the temperature on the wind speed (hereafter called corrected temperature). Wind speed and corrected temperature were standardized (centered and scaled). According to the bimodal activity pattern of mouflon, with two main peaks near dawn and dusk (Langbein et al. 1997; Pipia et al. 2008), we included the time (h) as a factor (24 modalities) in all models. We investigated the effects of time period, corrected tempera-

ture, wind speed, and the 3 two-way interactions among these factors on hourly pA (14 candidate models; see Table 1).

We fitted models on subsets of 124 data (i.e., approximately 4 data/day) randomly sampled out of the 744 (i.e., 24 data/day on 31 days) for each animal-year (activity data of the same animal were assigned to be independent between years) to limit the temporal autocorrelation among data (for a similar approach see Bourgoin et al. 2009). We selected a model from the set of candidate models using Akaike's information criterion with second-order adjustment to correct for small-sample bias (AIC_c). AIC_c provides a suitable way to find the best compromise between accuracy and precision (Burnham and Anderson 2002). More specifically, we computed AIC_c weights that correspond to the likelihood that a given model is the best given the data and the set of candidate models (Burnham and Anderson 2002, p. 172). We replicated this procedure 1000 times and computed mean AIC_c weights for each candidate model. We then computed the distribution of parameter estimates for the best model from the 1000 subsamples and used such distribution to make predictions. We predicted hourly pA for hourly median and the different combinations of the hourly extremes (i.e., 10% and 90% quantiles) corrected for temperature and wind speed. We computed mean pA for the different time periods. We predicted the timing of the end of the morning activity peak defined as the linearly extrapolated time between two successive predicted hourly pA at which pA = 0.3 for the first time after dawn. We similarly predicted the start of the evening activity peak as the linearly extrapolated time at which pA = 0.3 for the last time before dusk. We reported mean predicted values and confidence intervals (2.5% and 97.5% quantiles). Approximate tests of hypotheses were performed by comparing parameter distributions.

To assess the variability among females in hourly pA, we fitted a GLMM on the entire data set by including all the fixed effects selected from the best GLMM and computed the ratio between the variance of random terms and the sum of the random and residuals variances. All analyses were performed using libraries lme4 (Bates and Maechler 2010) and MASS (Venables and Ripley 2002) in R version 2.11.1 (R Development Core Team 2010).

Results

Model selection and individual variability

The best supported model (mean AIC_c weight = 0.654; Table 1) was the full model including all two-way interactions, whereas the second best supported model (mean AIC_c weight = 0.346) did not include the interaction between corrected temperature and wind speed. We chose to keep the full model for the subsequent analysis (between observed and predicted values, mean $R^2 = 0.46$; 95% CI = 0.43–0.48). Other models did not receive any support, emphasizing a marked time-of-day-specific effect of corrected temperature and wind speed on females' activity. As previously shown at a monthly scale (Bourgoin et al. 2008), random effects only accounted for a low proportion of the variance (0.9%), supporting the idea that females showed similar activity patterns.

Activity patterns under mild weather conditions

Under mild weather conditions (i.e., predictions based on

Table 1. Set of logistic regression models fitted to the predicted proportion of time active (pA) of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in relation to the time of day (time (h), 24 modalities), to the corrected temperature (i.e., residuals of the regression of the temperature on the wind speed; Tc), and to the wind speed (W) in July of 2003–2007.

Model	Mean AIC _c weight
Time + Tc + W + Time × Tc + Time × W + Tc × W	0.654
Time + Tc + W + Time × Tc + Time × W	0.346
Time + Tc + W + Time × W + Tc × W	0.000
Time + Tc + W + Time × Tc + Tc × W	0.000
Time + Tc + W + Tc × W	0.000
Time + Tc + W + Time × W	0.000
Time + Tc + W + Time × Tc	0.000
Time + W + Time × W	0.000
Time + Tc + Time × Tc	0.000
Time + Tc + W	0.000
Time + W	0.000
Time + Tc	0.000
Time	0.000
Null	0.000

Note: Models were ranked based on the mean weight of Akaike's information criterion with second-order adjustment to correct for small-sample bias (AIC_c). The selected model appears in boldface type.

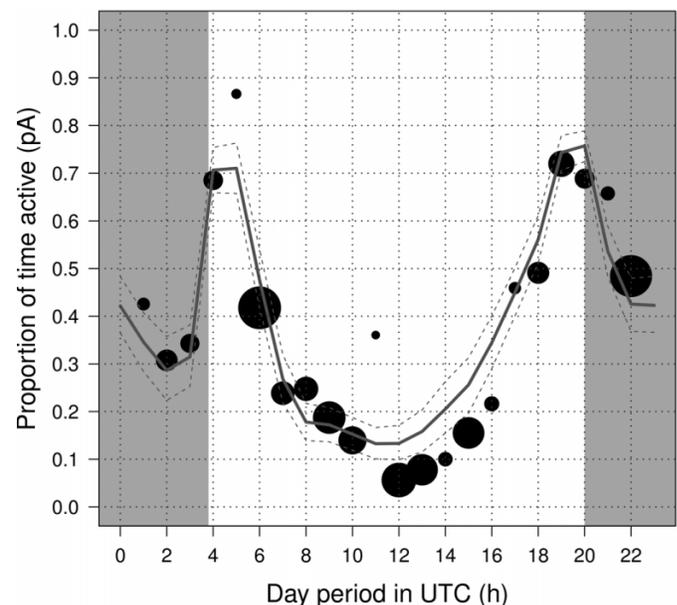
the hourly medians of the corrected temperature and wind speed), the 24 h pA (i.e., proportion of time active during a 24 h period) of females was of 0.38 (95% CI = 0.37–0.39). They had the same pA during diurnal and nocturnal periods (ratio of pA during the day (i.e., 0400–2000 UTC) vs. during the night (i.e., 2100–0300 UTC) = 0.96; 95% CI = 0.90–1.02; $p = 0.184$). We observed a typical 24 h bimodal activity pattern with two periods of intense activity at dawn and dusk (Fig. 1). Female mouflon markedly increased their activity at dawn and remained highly active during the 2 h following dawn (0400–0500 UTC; pA = 0.71; 95% CI = 0.68–0.74; Fig. 1). Then, they decreased their activity and spent most of their time inactive with the lowest pA observed around midday (0800–1600 UTC; pA = 0.19; 95% CI = 0.18–0.21). After this inactive period, females started around noon to spend more time active and reached a second activity peak during the 2 h preceding dusk (1900–2000 UTC; pA = 0.75; 95% CI = 0.73–0.77). The proportion of time active of females was higher during the evening peak (1900–2000 UTC) than during the morning peak (0400–0500 UTC; $p = 0.05$). Then, females decreased their pA to a lower level after dusk but remained quite active during the 2200–0000 period (pA = 0.42; 95% CI = 0.39–0.46). They continued to decrease their activity after midnight and the lowest pA during the night was observed at 0200 (pA = 0.29; 95% CI = 0.22–0.36).

Influences of weather conditions on the activity patterns

Influences on the bimodal activity pattern

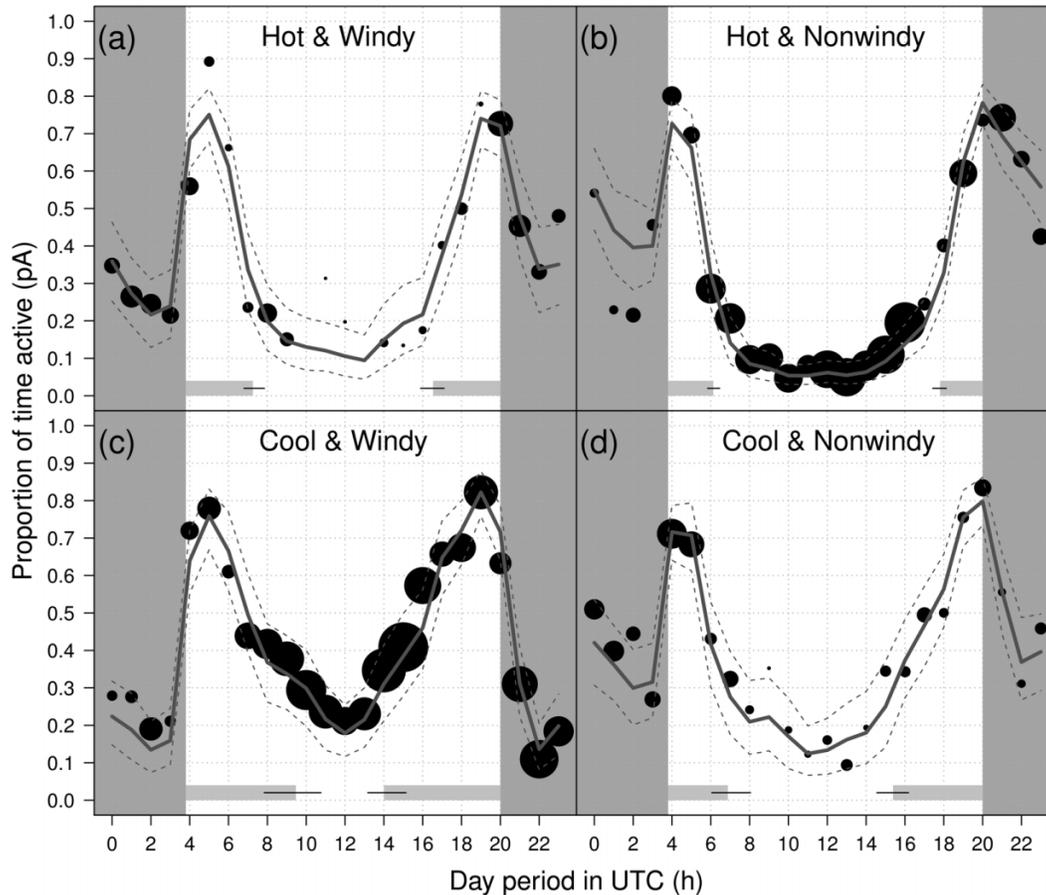
Whatever the corrected temperature and wind-speed conditions (i.e., predictions based on the 10% and 90% quantiles of the hourly observed corrected temperature (cool and hot, respectively) and hourly wind speed (nonwindy and windy, respectively)), we observed the same bimodal activity pattern with activity peaks near dawn and dusk (Figs. 2a–2d). Although the maximal value of pA during a hot windy eve-

Fig. 1. Activity patterns of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.) under mild climatic conditions (corrected for temperature and wind speed). Solid circles are mean observed values of the proportion of time active (pA) from GPS collars (1000 resampling) for the 40%–60% quantiles of the hourly observed corrected temperature and hourly wind speed in July of 2003–2007. Symbols are proportional to the sample size (mean from 1.2 to 5.7). Solid line (mean) and broken lines (2.5% and 97.5% quantiles) are predicted values of pA (1000 resampling; for the best model see Table 1) for the median hourly observed corrected temperature and the median hourly wind speed. Shaded areas represent the evening and the morning civil twilights.



ning (pA = 0.75; 95% CI = 0.69–0.81) tended to be lower compared with that of a cool windy evening (pA = 0.82; 95% CI = 0.76–0.88; $p = 0.072$; Figs. 2a and 2c), we did

Figs. 2a–2d. Effects of corrected temperature and wind speed on the 24 h activity patterns of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.). Solid circles are mean observed values of the proportion of time active (pA) from GPS collars (1000 resampling) for the different combinations of the <20% and >80% quantiles of the hourly observed corrected temperature (cool and hot, respectively) and hourly wind speed (nonwindy and windy, respectively) in July of 2003–2007. Symbols are proportional to the sample size (mean from 0.8 to 11.3). Solid line (mean) and broken lines (2.5% and 97.5% quantiles) are predicted values of pA (1000 resampling; for the best model see Table 1) for the 10% and 90% quantiles of the hourly observed corrected temperature (cool and hot, respectively) and hourly wind speed (nonwindy and windy, respectively) in July of 2003–2007. Horizontal light-shaded bars under each graph represent the mean ($\pm 95\%$ CI) computed time predicted values of the end time of the morning activity peak (i.e., time at which pA = 0.3 for the first time after dawn) and of the beginning time of the evening activity peak (i.e., time at which pA = 0.3 for the last time before dusk). Shaded areas represent the nocturnal period between the evening and the morning civil twilights.



not find any strong influence of climatic conditions on the maximal value of pA at the morning or at the evening peaks. No difference occurred in the maximal value of pA between the morning and the evening peaks for any climatic condition (from 0.72 (95% CI = 0.68–0.77) to 0.82 (95% CI = 0.76–0.88); all $p > 0.114$).

However, climatic conditions influenced the timing of the activity peaks, with the most pronounced difference occurring between cool windy and hot nonwindy days. Peaks occurred at dawn and dusk (ca. 0400 and 2000 UTC, respectively) during hot nonwindy days, whereas they occurred 1 h after dawn and 1 h before dusk during cool windy days (ca. 0500 and 1900 UTC, respectively; Figs. 2b and 2c).

Corrected temperature influences

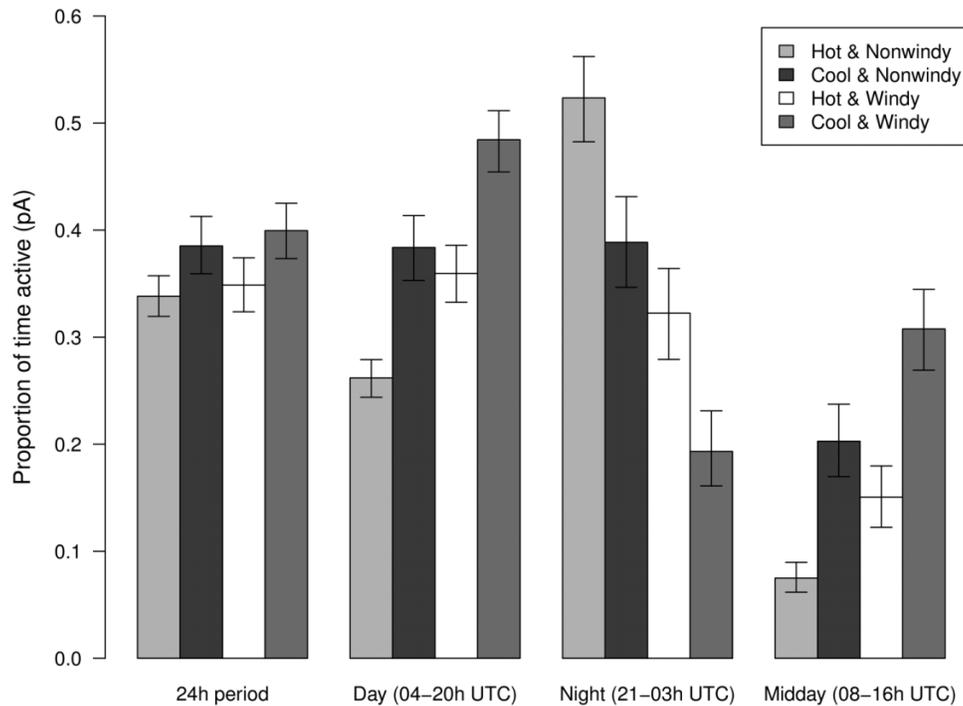
Climatic conditions influenced the 24 h pA of mouflon, with females being less active during hot days compared with cool days under similar wind conditions (windy days: $p = 0.010$; nonwindy days: $p = 0.016$; Fig. 3). This lower 24 h pA during hot days was explained by a lower diurnal

activity (all $p < 0.001$) that was not fully counterbalanced by the observed higher nocturnal activity (all $p < 0.001$; Fig. 3). Females remained highly active during less time after dawn (time at which pA = 0.3 for the first time after dawn; windy days: $p = 0.002$; nonwindy days: $p = 0.064$; see horizontal light-shaded bars in Figs. 2a and 2c, 2b and 2d), had a lower pA around midday (0800–1600 UTC; all $p < 0.001$; Fig. 3), and started later to increase their activity at evening (time at which pA = 0.3 for the last time before dusk: all $p < 0.001$; Figs. 2a and 2c, 2b and 2d) during hot days than during cool days.

Wind speed influences

Wind speed had no influence on the 24 h pA during hot ($p = 0.562$) or cool ($p = 0.532$; Fig. 3) days. Wind led to a higher diurnal activity and to a lower nocturnal activity of females during hot and cool days (all $p < 0.001$; Fig. 3). It allowed females to remain highly active during a longer period after dawn (time at which pA = 0.3 for the first time after dawn: all $p \leq 0.012$; see horizontal light-shaded bars in

Fig. 3. Effects of corrected temperature and wind speed on the proportion of time active (pA) of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.) during 24 h, day, night, and midday periods. Bars represented mean ± 95% CI activity pA estimates predicted (1000 resampling) from the best selected model (model in boldface type in Table 1). For further details see Figs. 2a–2d.



Figs. 2a and 2b, 2c and 2d), to be more active around midday (all $p < 0.001$; Fig. 3), and to start earlier to increase their activity at evening (time at which pA = 0.3 for the last time before dusk: all $p \leq 0.032$; Figs. 2a and 2b, 2c and 2d) than during nonwindy days.

Corrected temperature and wind speed influences

In agreement with our hypotheses of the influence of summer climatic conditions on activity patterns of females, the most pronounced differences occurred between hot nonwindy days and cool windy days. Females were less active (24 h pA) during hot nonwindy days than during cool windy days ($p < 0.001$), with a lower diurnal and a higher nocturnal activities (all $p < 0.001$; Fig. 3). They were highly active during a longer period after dawn (time at which pA = 0.3 for the first time after dawn: all $p < 0.001$; see horizontal light-shaded bars in Figs. 2c and 2b), had a higher pA around midday ($p < 0.001$; Fig. 3), and increased earlier their activity at evening (time at which pA = 0.3 for the last time before dusk: $p < 0.001$; Figs. 2c and 2b) during cool windy than during nonwindy hot diurnal periods.

Females were less active (24 h pA) during hot windy days than during cool nonwindy days ($p = 0.040$; Fig. 3) with a tendency to be less active during hot windy nights ($p = 0.062$), but no difference occurred in the diurnal period ($p = 0.216$; Fig. 3). A similar diurnal duration of morning peaks (time at which pA = 0.3 for the first time after dawn: $p = 0.498$; see horizontal light-shaded bars in Figs. 2d and 2a) occurred, but peaks at evening tended to start earlier (time at which pA = 0.3 for the first time before dusk: $p = 0.060$; Figs. 2d and 2a) during cool nonwindy days than during hot windy days. The proportion of time active was higher around midday during cool nonwindy days than during hot windy days ($p = 0.032$; Fig. 3).

Females had the same pA during the diurnal period and the nocturnal period during hot windy days (ratio of pA during the day and during the night: 1.12; 95% CI = 0.98–1.28; $p = 0.100$) and cool nonwindy days (0.99; 95% CI = 0.88–1.11; $p = 0.822$). They were far more active during daytime of cool windy days (2.53; 95% CI = 2.12–2.99; $p < 0.001$), whereas the nocturnal activity predominated during hot nonwindy days (0.50; 95% CI = 0.46–0.55; $p < 0.001$).

Discussion

We found a strong influence of corrected temperature and wind speed on the activity pattern of female mouflon during summer even if our meteorological data were recorded 13 km from our study area. We probably could have explained more variation in the data by using a local measure of climate, because climatic variables such as wind speed could be highly variable depending on what part of the landscape the animals stood. Similarly, other biologically relevant factors (e.g., group size; Beauchamp 2007) were not included in our analysis because these data were not available. Nonetheless, the best model selected accounted for more than 45% of the variation in the data, providing clear support for the importance of large-scale climatic conditions in shaping activity pattern of female mouflon.

We found a typical bimodal activity pattern of female mouflon with two marked periods of intense activity near dawn and dusk separated by a period of low activity (Fig. 1). This bimodal pattern has been previously documented in other mouflon (Germany: Langbein et al. 1997; Kerguelen archipelago: Moncorps et al. 1997; Sardinia, Italy: Pipia et al. 2008) and ungulate (e.g., red deer: Georgii 1981; white-tailed deer: Beier and McCullough 1990; moose (*Alces alces* (L., 1758)): Cederlund 1989) populations. We observed

that the two periods of intense activity consistently occurred despite the variation in temperature and wind speed (Fig. 2; in agreement with H1). Only the duration of the periods of intense activity and the timing of peaks changed in response to climate. Female mouflon were the most active 1 h earlier and during less time in the morning while they started later to increase their activity and were the most active 1 h later in the evening during hot nonwindy days compared with cool windy days, respectively (for the duration of the periods of intense activity in agreement with H2a and H3a). The bimodal pattern of activity was most pronounced under constraining climatic conditions, as mouflon decreased their midday activity during hot nonwindy days compared with cool windy days (in agreement with H2b and H3b).

Although previous studies have reported a higher activity rate of mouflon at night than during the day in summer at the monthly scale (Langbein et al. 1997), we found a wide range of day to night activity ratio (0.50–2.53), with females being either mostly diurnal or mostly nocturnal in response to climatic conditions. Mouflon can be primarily seen as a diurnal species because the majority of the female activity occurred during the day under less thermally constraining climatic conditions (i.e., cool temperature and high wind speed; day to night ratio of the proportion of time active: 0.86; 95% CI = 0.84–0.88; Fig. 3).

We found that mouflon decreased their diurnal activity during hot days (in agreement with H2c) and concurrently increased their nocturnal activity (in agreement with H2d). Nocturnal activity also offers the benefit during hot days of foraging on wet vegetation owing to water condensation (Cain et al. 2006). Although wind speed had no effect on 24 h female activity, females were more active during the day (in agreement with H3c) and less active at night of windy days than nonwindy days (in agreement with H3d). This result emphasizes the importance of working at different temporal scales to study the variation in activity patterns of large herbivores (Scheibe et al. 1999). Beyond the heat loss by convection, wind might also positively influence female activity by decreasing insect harassment (Langbein and Scheibe 2001).

The variation in activity we reported here supports the idea that mouflon adjust their time budget to limit thermal stress. Such an adaptation may operate through 4 mechanisms: (1) decreasing earlier the morning activity; (2) being less active and during a longer period around midday; (3) starting later the evening activity period with a higher proportion of the evening activity performed at night; and (4) being more active at night when faced with worst conditions (i.e., hot nonwindy days). In white-tailed deer, increasing temperatures similarly lead animals to decrease their activity at dawn, dusk, and especially daytime while they increased their nocturnal activity (Beier and McCullough 1990). In Italy, male and female mouflon (Pipia et al. 2008) markedly decrease their activity around midday during hot days, and also in the evening for the Alpine ibex (*Capra ibex* L., 1758) (Aublet et al. 2009).

We can expect that the benefit of spending more time foraging is mitigated by heat production (i.e., leading to a lower 24 h active time: Belovsky and Slade 1986; Beier and McCullough 1990). Hence, thermally stressing conditions may lead mouflon to adopt a time-minimizer (sensu Schoener

1971) foraging tactic (i.e., minimizing the time spent in muscular and foraging activities to fulfill minimum energetic requirement) rather than to adopt an energy-maximizer tactic. We effectively observed female mouflon to be 15.3% less active (i.e., approximately 1 h and 30 min over 24 h) during hot nonwindy days compared with cool windy days (Fig. 3), with an activity restrained to the coolest periods of the day (dawn, dusk, and night). However, further studies focusing specifically on foraging behavior under thermally stressing conditions would be required to assess fully this hypothesis.

This active time restriction is not necessarily associated with low resource acquisition because animals may compensate shorter feeding time by increasing instantaneous intake rate (Iason et al. 1999), as well as spending less time in vigilance at night than during the diurnal period (Beauchamp 2007). However, several lines of evidence suggest that female mouflon would not have the opportunity for such compensation. First, potential for compensation is limited under low resource availability (Iason et al. 1999), as commonly encountered during summer droughts in Mediterranean areas. Second, female mouflon are expected to give birth each year (Garel et al. 2005) and to have quite high reproductive success so that most females were likely to have one lamb at heel during the summer. Hence, females have to increase foraging effort to meet increased energy expenditures required for raising offspring (Ruckstuhl and Festa-Bianchet 1998). They were thus unlikely to increase even more their intake rate to compensate for the time restriction (because of physiological constraints, e.g., maximal bite rate, rumen size).

Hence, a lower time spent active owing to heat should lead to a lower total daily food intake during a hot day compared with a less thermally stressing day, especially for females raising offspring. Ensuing starvation should not jeopardize individual performance if short (e.g., 1–2 successive days). However, consecutive weeks of heat and drought are not exceptional events in Mediterranean areas (Paeth and Hense 2005), which may lead to impaired resource acquisition over the long term and thus individual performance (Stephens and Krebs 1986; mouflon: Garel et al. 2004). Moreover, starvation is only one of the many negative effects of physiological stress caused by heat on the individuals' life-history traits. In a global warming context, long-term studies of the variation in the activity pattern of individuals are thus of particular interest to detect critical events for population dynamic.

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