



Original Article

# Sex-specific adjustments in habitat selection contribute to buffer mouflon against summer conditions

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In the context of global warming, investigating how animals buffer against the hottest conditions is a crucial issue. We focused on habitat selection in a French Mediterranean mouflon population during 2010–2012 summers. Using locations and temperatures recorded on GPS-collared individuals, we assessed thermal cover provided by different habitats and analyzed sex- and scale-specific habitat selection and its thermal consequences for mouflon. At the home range scale, females ( $n = 26$ ) avoided unsafe plateaux and selected steep refuges, trading off thermal cover with better conditions for lamb survival. Larger males ( $n = 18$ ), not constrained by young rearing and expected to respond more strongly than smaller females to hot conditions, rather selected forests on plateaux providing thermal cover. In terms of movements, both sexes selected forests during hottest days. Males also took advantage of food and thermal cover provided by moorlands on plateaux until twilight, whereas females traded off food and thermal cover with refuges. Thermal cover significantly influenced habitat selection when temperature at the closest weather station exceeded 17.1 °C (95% confidence interval = 14.9–19.7) in males and 15.5 °C (95% confidence interval = 13.9–16.5) in females. Above these thresholds, ambient temperatures experienced by mouflon increased more slowly than temperatures at the weather station (males: 0.77 °C [95% confidence interval = 0.74–0.79] per 1 °C rise at the weather station, females: 0.75 °C [95% confidence interval = 0.73–0.76]) and more slowly than below these thresholds (males: 0.89 °C [95% confidence interval = 0.85–0.93], females: 0.94 °C [95% confidence interval = 0.89–0.98]). These findings suggested that habitat selection contributes to buffer mouflon against summer conditions but raised questions on energetic and fitness costs in areas where summer temperatures are predicted to increase further.

**Key words:** behavioral thermoregulation, GPS collars, *Ovis gmelini musimon* × *Ovis sp.*, temperature threshold, thermal cover, thermal sensors.

## INTRODUCTION

In the context of global warming, understanding how climate variations shape animals' behavior and consequently affect population dynamics and species' distribution is a crucial issue to predict the consequences of ongoing changes in climate on ecosystems structure and functioning (Huey and Tewksbury 2009; Tuomainen

and Candolin 2011). In the northern hemisphere, research often focused on winter as climate is harsh and food is scarce during this season (Weladji et al. 2002; Sæther et al. 2004). However, following the temperature rise observed in the last decades, recent studies now also focus on demographic (e.g., Garel et al. 2004; Jiguet et al. 2006) and behavioral consequences (e.g., Melin et al. 2014; Scheffers et al. 2014; Shrestha et al. 2014) of high temperatures, heat waves, and summer droughts, whose frequency and intensity are predicted to increase further in a near future (Intergovernmental Panel on Climate Change 2013).

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Two types of responses allowing homeotherms to maintain body temperature within tolerable limits under inhospitable thermal conditions have been experimentally identified: behavioral and autonomic (e.g., involuntary thermoeffector responses as sweating) thermoregulation (IUPS Thermal Commission 2001). Though rarely checked in the field, experimental analyses showed that both types of thermoregulation are generally controlled by the overrun of critical temperature thresholds (Maloney et al. 2005; Terrien et al. 2010). However, behavioral thermoregulation being less costly and sustainable longer than autonomic responses (Maloney et al. 2005; Terrien et al. 2010) should be the primary mechanism by which animals buffer against inhospitable thermal conditions. For instance, when temperatures exceed critical thresholds, large herbivores adjust their thermogenic foraging activities and increase the selection of habitats providing thermal cover (e.g., Owen-Smith 1998; van Beest et al. 2012). Through behavioral thermoregulation, climatic conditions can, therefore, strongly affect large herbivores' habitat selection and become a major driver not only of individual energetic balance but also of herbivores–habitats relationships, with potential cascading effects on landscape dynamics (Jones et al. 1994).

In large herbivores, habitat selection is a complex hierarchical process largely driven by a pervasive food/cover trade-off arising from the common segregation between foraging resources and conditions providing cover from perceived predation risk or from adverse weather (Lima and Dill 1990; Mysterud and Ostbye 1999). It has been proposed that the spatiotemporal scale at which a specific resource or condition drives habitat selection may reflect the importance of this resource or condition in terms of fitness (Rettie and Messier 2000). In addition, the activity pattern of ruminants is characterized by successive foraging and ruminating/resting bouts (Belovsky 1981; Gillingham et al. 1997) during which specific resources and conditions should be required. Accordingly, fine-scale habitat use/selection and activity may be closely related in space and time (e.g., Bjørneraas et al. 2011). Responses in habitat selection of ruminants to adverse thermal conditions could hence occur not only when critical thresholds are overrun but also concurrently with temporal, and possibly compensatory, shifts in daily activities (Schoener 1971; Belovsky 1981).

Individuals' own traits and states (e.g., sex, reproductive status), which determine energy requirements and susceptibility to risk factors, are also major determinants of large herbivores' habitat selection (e.g., Bjørneraas et al. 2011). Due to differences in allometric relationships between body size and several morphophysiological characteristics of large herbivores (e.g., intake rate, gut capacity, and retention time), their ecology and their behavior are in particular largely related to their size (Geist 1974) and hence to their sex in dimorphic species (Ruckstuhl and Neuhaus 2006). Larger individuals/species having higher thermal inertia and lower conductance than smaller ones as a result of lower surface to volume ratios (Porter and Kearney 2009) should thus respond more strongly under adverse thermal conditions (Broders et al. 2012; Shrestha et al. 2014). It is also expected that larger individuals/species have lower relative energetic demands than smaller ones and hence benefit from a higher flexibility to allocate time under hot conditions (Aublet et al. 2009). But surprisingly, although these differences have been hypothesized for a long time to explain sexual habitat segregation in dimorphic species under cold/northern conditions (“weather sensitivity hypothesis,” Conrard et al. 2000), few studies investigated responses to hot summer conditions in habitat use/selection of sex-structured populations despite the importance

of habitat segregation for the conservation and the management of dimorphic herbivores and of their habitats (Rubin and Bleich 2006).

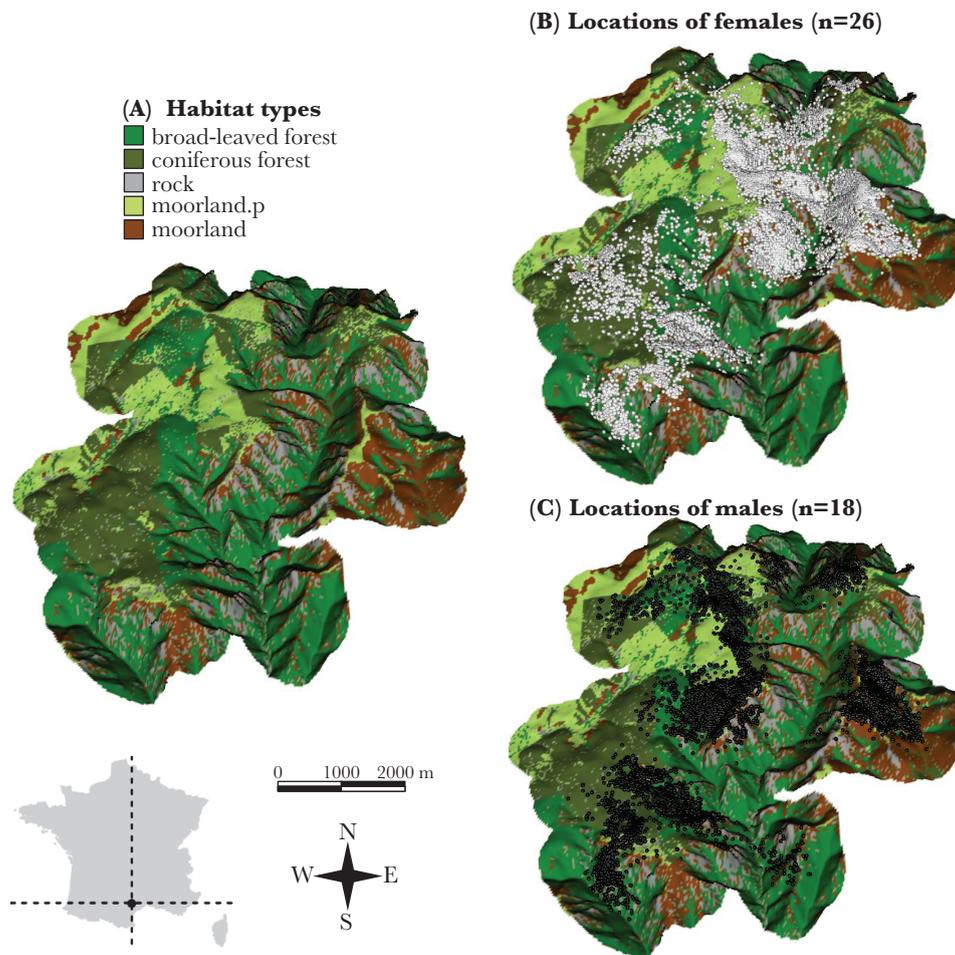
In the Caroux-Espinouse massif (southern France), hot and dry summers have been identified as important determinants of the dynamics of the Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. population (Garel et al. 2004). Behavioral thermoregulation has also been revealed on the activity pattern of females (Bourgoin et al. 2011). We aimed here at determining whether habitat selection allowed both sexes of this dimorphic herbivore to cope with thermal constraints in addition to the other components of the food/cover trade-off. Using ambient temperatures derived from sensors embedded in GPS collars fitted on 44 mouflon (26 females and 18 males), we first defined a “thermal landscape” as experienced by animals under the hottest weather conditions (i.e., hot and nonwindy; defined based on data from the closest weather station) in habitat types also differing in terms of foraging conditions and protection against perceived predation risk. We then analyzed whether the thermal properties of each habitat type emerged as a driver of habitat selection at broad scale, that is, choice of home range within available landscape, and at fine scale, that is, decisions concerning movement steps. At fine scale, we more specifically investigated changes in habitat selection under contrasted weather conditions (i.e., cool and windy, and hot and nonwindy), and between day, twilight, and night, to test whether such changes only occurred during the hottest day periods, when the critical thermal threshold was most probably overrun, or also concurrently with shifts in daily activities. We finally assessed the variation in ambient temperatures experienced by animals according to reference temperatures recorded at the closest weather station to evaluate the thermal consequences of habitat selection for both sexes. This latter analysis allowed us to check for the existence of a temperature threshold beyond which thermal cover emerged as a main driver of habitat selection (Maloney et al. 2005; Terrien et al. 2010).

Given the importance of large herbivores' body size in their responses to high temperatures (Aublet et al. 2009; Broders et al. 2012; Shrestha et al. 2014), and of the sexual size dimorphism in Mediterranean mouflon (males: 35–50 kg; females: 25–35 kg; percentage of body mass difference between both sexes: 29% and 41% of males and females average body mass, respectively; Garel et al. 2007), we expected larger males to respond to hot summer conditions at broader scale and/or more strongly than smaller females. At fine scale, we expected thermal cover to drive mouflon habitat selection in particular during hottest days, that is, when the critical temperature threshold controlling thermoregulation was most probably overrun. During this period and above this temperature threshold, habitat selection may allow ambient temperature experienced by both sexes to increase more slowly than the reference temperatures recorded at the weather station. Finally, given that females of our population were also found more active during hottest nights (Bourgoin et al. 2011), we expected mouflon to select for the habitat types providing the best foraging conditions during these periods.

## MATERIALS AND METHODS

### Study area and environmental conditions

We collected data in the Caroux-Espinouse study area (43°38'N, 2°58'E, 3550 ha, 390–1124 m a.s.l., Figure 1) in southern France. Hourly temperature and wind speed were recorded during 2010–2012 summers (July–August) by Météo France at the Fraisse-Murat



**Figure 1**

(A) Three-dimensional land cover map of the Caroux-Espinouse study area (390–1124 m a.s.l., 3550 ha, southern France), where sex-specific summer habitat selection of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) was studied during 2010–2012 summers (July–August). The position of the study area in France is given in bottom left panel. The locations of the 44 GPS-collared Mediterranean mouflon (B: gray = 26 females; C: black = 18 males) during the corresponding period are represented in the right panels.

weather station situated on the upper part of the study area (43°38'N, 2°49'E; 1022 m a.s.l., 10 km east, 10 m above the ground). Preliminary analyses supported the relevance of these weather data to assess the local weather experienced in the studied population: the station was within the altitudinal range occupied by mouflon and we found a strong correlation ( $r = 0.98$ ) with daily data ( $n = 2745$ ) recorded by another weather station included in the population range (6 km east). Summers were generally hot (average [standard deviation, SD] temperatures at 1022 m a.s.l. in 2010, 2011, and 2012: 17.0 [4.3], 15.7 [4.3], and 17.0 [4.7] °C, respectively; Table 1) and dry (precipitations in 2010, 2011, and 2012: 41.0, 96.7, and 140.3 mm, respectively), with frequent and dominant north-north-west winds (percentage of days with wind speed >3 m/s in 2010, 2011, and 2012: 75%, 72%, and 71%, respectively; Baudière 1962).

The topography of this low mountain area is characterized by a deep north-south-oriented valley indenting windswept plateaux (altitude > 900 m a.s.l. and slope < 10°; Figure 1). If not exploited for coniferous forestry (*Pinus sylvestris*, *Pinus nigra*, and *Picea abies*), plateaux are mainly composed of moorlands (mostly heather *Erica cinerea* and *Calluna vulgaris*, and broom *Cytisus oromediterraneus* and *Cytisus scoparius*), pastures, meadows, and artificial cultures providing abundant food for mouflon (*Brachypodium sylvaticum*, *Festuca rubra*, *Festuca paniculata*, *Festuca ovina*, *Carex* sp.; Baudière 1970; Marchand

**(B) Locations of females (n=26)**



**(C) Locations of males (n=18)**



**Table 1**

**Average temperature (°C [SD]) and wind speed (m/s [SD]) recorded at the closest automatic weather station to our study area (Météo France, Fraïsse-Murat; 1022 m a.s.l., 10 m above the ground, 10 km east from the study area) according to day period and weather conditions during 2010–2012 summers (July–August, see Table 1 and Supplementary Table S1 for details)**

Day period	Weather conditions	Temperature (°C)	Wind speed (m/s)
Day	Cool-windy	13.6 [2.5]	8.1 [1.3]
	Hot-nonwindy	23.3 [2.7]	2.5 [0.8]
Twilight	Cool-windy	11.4 [2.3]	7.5 [1.2]
	Hot-nonwindy	19.4 [2.5]	1.9 [0.8]
Night	Cool-windy	10.7 [1.5]	7.5 [1.3]
	Hot-nonwindy	18.4 [1.8]	1.8 [0.7]

et al. 2013) but generally perceived as risky by wild sheep because of low slope, high distance to refuge areas and high exposure to potential predators (Hopewell et al. 2005; Singh et al. 2010). Slopes that are perceived as safer, are either covered by heather and broom moorlands, by broad-leaved trees (mainly beech *Fagus sylvatica*, chestnut trees *Castanea sativa*, and evergreen oak *Quercus ilex*), or are essentially steep rocky areas constituting refuges from

perceived predation risk (Risenhoover and Bailey 1985; Wakelyn 1987). We distinguished 5 habitat types differing in terms of foraging conditions, of protection against perceived predation risk and potentially providing contrasted situations regarding thermal cover due to the vegetation cover and the position on slopes or on “high” plateaux (i.e., >900 m and slope  $\leq 10^\circ$ , noted with “.p” in acronyms): rocky area, moorland, moorland versus moorland.p, and forest (85% being broad-leaved trees) versus “forest.p” (71% being coniferous trees; see Table 2 for a summary of these characteristics). We derived habitat types from the processing (K-means unsupervised classification) of a Satellite Pour l’Observation de la Terre satellite image taken in July 2005 and field validation in a 25 m  $\times$  25 m grid (Tronchot 2008). We characterized each pixel by the dominant habitat type. We derived altitude and slope from a digital elevation model (resolution = 25 m; source: ©BD ALTI data set from the Institut Géographique National).

### Mouflon population and GPS data

The population of Mediterranean mouflon inhabiting this massif originated from 19 individuals (9 males and 10 females) released between 1956 and 1960 but is now harvested from the beginning of September to the end of February (around 500 individuals per year during the study period). It has been monitored by the Office National de la Chasse et de la Faune Sauvage since 1974 according to the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009-014) in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94-1). Mouflon are caught and marked annually between May and July, using traps and drop nets baited with salt licks.

Between 2010 and 2012, we equipped 26 adult females and 18 adult males ( $\geq 2$  years old; average body mass of GPS-collared individuals weighted when trapped [SD]: females [ $n = 23$ ]: 24.1 [2.5] kg; males [ $n = 17$ ]: 30.1 [5.3] kg) with Lotek GPS collars 3300S (revision 2; Lotek Engineering Inc., Carp, Ontario, Canada). We scheduled GPS collars deployed in 2010 (10 females and 6 males) to record animal locations every other even hour, allowing the monitoring to be prolonged during whole 2011 summer for 4 males and 3 females. We scheduled GPS collars deployed in 2011 (7 females and 4 males) and 2012 (9 females and 8 males) to record locations every 2 h alternating between even hours on one day (from 0 to 22 h UTC) and odd hours on the following day (from 1

to 23 h UTC, hence including one 3 h and one 1 h trajectory each 48 h) but to stop before the second summer. We, hence, derived our data set from 51 “mouflon-year” (29 females and 22 males). We screened GPS data for positional outliers ( $n = 77$ ; 0.26% of the full data set) based on unlikely movement characteristics (Bjørneraas et al. 2010) and only included 2 h nonerroneous locations in analyses. In addition, all GPS collars were equipped with a sensor recording local temperature during each location attempt (but one failed on a female in 2010). This sensor was embedded in a board house covered with a 2-4 cm layer of foam that prevented the board house from direct contacts with animal fur and skin. However, as the radiant body heat of animals influenced data recorded by thermal sensors embedded in GPS collars, we derived ambient temperatures from sensor data using the relationship experimentally established by Jiang et al. (2012) on the same model of GPS collars:  $T_{\text{ambient}} = (T_{\text{sensor}} - 0.156 \times T_{\text{animal}} + 0.128) / (1 - 0.156)$ , with  $T_{\text{ambient}}$  = ambient temperature,  $T_{\text{sensor}}$  = temperature recorded by sensors embedded in GPS collars fitted on mouflon, and  $T_{\text{animal}}$  = body temperature of animals, that is, 39.1 °C for mouflon (Dwyer 2008). Although our correction did not allow controlling for animal position when temperatures were recorded (e.g., laying with the neck covering temperature sensor vs. standing) or for direct sunlight influence on the GPS board house, we expected that the ambient temperatures derived from these sensors would be a positively biased measure of local temperature. This bias reduced our ability to detect thermal cover provided by the different habitat types, and we, hence, expected our results to be conservative. Furthermore, given the range of the normal variation in internal temperature of sheep ( $\pm 0.8$  °C, Dwyer 2008), we expected their resulting influence on ambient temperatures derived from sensors ( $\pm 0.15$  °C based on the relationship established by Jiang et al. 2012) to be negligible.

Among the 26 GPS-collared females, 24 were lactating when captured and 18/20 were seen at least once with a lamb during the studied summer(s). Besides, postmortem analysis of harvested females showed that a high proportion of females reproduce every year in this population (91% of adults, Garel et al. 2005) suggesting that most GPS-collared females were likely to have a lamb at heel during the study period.

Roe deer and wild boar (at low density comparatively to mouflon) were the 2 other free-ranging ungulates inhabiting this massif. Mouflon had no natural predators in the study area, except for free-roaming dogs, golden eagles (*Aquila chrysaetos*), and red foxes (*Vulpes vulpes*) that may occasionally predate newborns and sick mouflon.

**Table 2**

**Characteristics of the 5 habitat types defined to study habitat selection of Mediterranean mouflon (*Ovis gmelini musimon*  $\times$  *Ovis* sp.) during 2010–2012 summers (July–August) in the Caroux-Espinouse study area (southern France; see Study area and environmental conditions and Figure 2 for details)**

Habitat types	Foraging conditions	Protection against perceived predation risk	Thermal cover (during hottest days)
Moorland.p	++	--	++
Forest.p	0	–	+
Moorland	+	–	0
Rock	–	++	--
Forest	0	+	0

“+” corresponds to a high value, “–” to a low value, and “0” to a neutral effect.

### Statistical analyses

#### *Thermal cover assessment in the different habitat types*

We focused the assessment of thermal cover on the hottest conditions from studied summers that we identified using data recorded at the closest weather station. As temperature and wind speed were strongly correlated in our study area ( $r$  ranged from  $-0.49$  to  $-0.55$  according to day period, with all  $P$ -values  $< 0.001$ ), we determined hottest conditions (i.e., hot and nonwindy) using one-third (wind) and two-third (temperatures) quantiles of their hourly distributions (see Table 1 and Supplementary Table S1 for details). We then investigated differences in thermal properties of the 5 habitat types based on ambient temperatures derived from sensors. We performed period-specific analyses (i.e., days, twilights, and nights; see Habitat selection at fine scale for details) because the thermal properties of the different habitats were expected to vary at the daily scale (van Beest et al. 2012; Melin

et al. 2014). We compared the whole set of ambient temperatures experienced by the monitored individuals within each habitat type during a specific period (on average 315 [range = 26–1300] records per habitat type and per period) using Anovas and post hoc paired Tukey honest significant difference tests to determine the habitat type(s) where differences in thermal properties occurred.

### Habitat selection at broad scale

We related the composition of the summer home range of each mouflon-year to the proportions of each habitat type in the available landscape using selection ratios (Manly et al. 2002). We computed home range boundaries using fixed 95% kernel with an ad hoc method for smoothing parameter (Worton 1989). We considered availability as the same for all individuals and defined it as the 500 m buffer around the whole set of GPS locations, a distance including >95% of distances travelled by GPS-collared mouflon in 2 h. We tested for differences between both sexes using linear mixed-effects models including mouflon identity and year as non-nested grouping factors (random intercept models) to account for repeated measurements on the same individuals and potential between-years differences in selection criteria, respectively. We compared models including sex, habitat type, and their interaction using Akaike's information criterion ( $AIC_c$ ) with second-order adjustment to correct for small sample bias (Burnham and Anderson 2002). Following Burnham and Anderson (2002), models were ordered from the best to the least supported model (lowest to highest  $AIC_c$ ), and we considered 2 competing models as different when their difference in  $AIC_c$  (hereafter called  $\Delta AIC_c$ ) was >2. We also assessed the strength of evidence in favor of one model over the others by computing Akaike weights  $w_i$ . They can be interpreted as the probability that a model is the best model given the data and the set of candidate models. We then considered each habitat type as selected or avoided when the 95% confidence interval (95% CI) predicted by the selected model was higher or lower than 1, respectively, that is, the threshold indicating that use equals availability. Similarly, we considered nonoverlapping 95% CI within and between habitat types and sexes as significantly different.

### Habitat selection at fine scale

We analyzed patterns of fine-scale habitat selection under 2 contrasted weather conditions, that is, cool and windy (determined using one-third and two-third quantiles of temperature and wind speed hourly distributions) and hot and nonwindy (previously defined, see Table 1 and Supplementary Table S1). We also considered 3 day periods based on the bimodal activity rhythm of mouflon described in this population during summer (Bourgoin et al. 2011), which we expected to generate circadian variation in habitat selection (Marchand P, Garel M, Bourgoin G, Dubray D, Maillard D, Loison A, unpublished data, and see Bjørneraas et al. 2011 for an example in another ungulate species). We contrasted twilight (4–6 and 18–20 h UTC), that is, when mouflon were mostly active, with day (7–17 h UTC) and night (21–3 h UTC) periods.

We assessed habitat selection using step selection functions (SSFs), a particular case of resource selection functions allowing investigating habitat selection at the scale of movement steps (Fortin et al. 2005; Thurfjell et al. 2014). We coupled each observed GPS location with 10 random locations considered as available according to the area used by an individual at that time. We sampled random locations from around observed locations using the observed step length and turning angle distributions from each sex for the corresponding day period (Fortin et al. 2005). We compared

habitat characteristics under observed and random locations using conditional logistic regression and a matched case-control design (Hosmer and Lemeshow 2000). We computed sex- and period-specific conditional logistic regressions including habitat types, weather conditions (i.e., cool and windy vs. hot and nonwindy), and their interactions as explanatory variables. They provided coefficients representing the log odds ratios for a habitat being chosen relative to a reference habitat for which  $\beta = 0$ , that is, moorland in slopes in our analyses (providing the more explicit graphical representation of the results). Dividing the data into time periods decreased autocorrelation within the data set because each individual was sampled only a few times within each period (Roever et al. 2010). However, we accounted for the nonindependence of telemetry locations from the same individual by computing robust standard errors using the clustering procedure proposed by Forester et al. (2009). Nonoverlapping 95% CI (based on robust standard errors) within and between habitat types across weather conditions indicated significant differences in habitat selection. As such, selection or avoidance for the reference habitat type occurred when the other habitat types have 95% CI <0 or >0, respectively.

### Thermal consequences of habitat selection during the day and temperature threshold

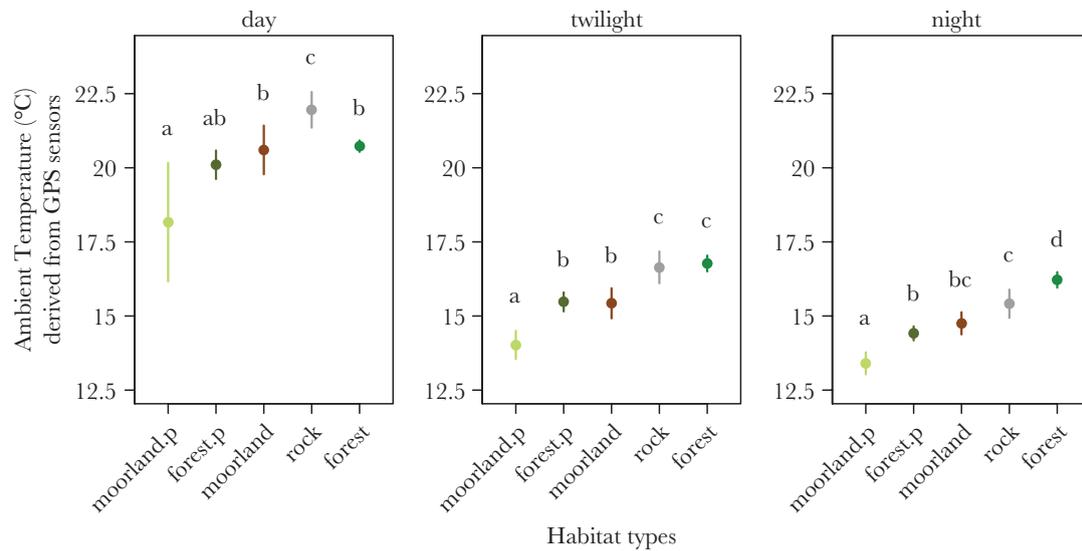
We modeled the variation in ambient temperatures experienced by animals (i.e., derived from thermal sensors) according to temperatures recorded at the closest weather station to assess the thermal consequences of habitat selection of both sexes during the hottest conditions (i.e., during the day). This also allowed us to check for the existence of a temperature threshold beyond which thermal cover emerges as a main driver of mouflon habitat selection. We used mixed-effects models including mouflon identity and year as non-nested grouping factors (random intercept models) to account for repeated measurements on the same individuals and potential between-year differences in the relationships between both variables, respectively. Based on  $AIC_c$  and the same decision rules as previously described (see Habitat selection at broad scale in Statistical analyses), we compared models considering no relationship (i.e., null model) or linear, quadratic (linear mixed-effects models), nonlinear (general additive mixed models), or threshold-dependent (piecewise mixed-effects models) relationships between both variables. We determined the threshold temperatures from piecewise models (a common threshold for both sexes or sex-specific thresholds) and their 95% CI by minimizing the deviance of the corresponding models and from profile likelihood, respectively (Hansen 2000). We penalized  $AIC_c$  values of piecewise models with additional degree(s) of freedom to account for the previous estimation of the threshold temperature(s). We also tested for additive and interactive effects of sex in these relationships.

We performed all analyses using R version 3.0.2 (R Development Core Team 2013), packages “adehabitatMA,” “adehabitatHR,” “adehabitatHS,” and “adehabitatLT” (Calenge 2006) for the computation of habitat variables, home ranges and landscape compositions, selection ratios, and movement characteristics, respectively, and package “lme4” and “mgcv” for mixed-effects modeling procedure (Wood 2006; Bates et al. 2011) and “survival” for SSFs (Therneau 2013).

## RESULTS

### Thermal cover assessment in the different habitat types

As a general rule, ambient temperatures experienced by GPS-collared mouflon under the hottest conditions increased from



**Figure 2**

Average (95% CI) ambient temperature (°C) experienced by Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.; 26 females and 18 males) in the different habitat types from the Caroux-Espinouse study area (southern France) according to day period during the hottest conditions (i.e., hot and nonwindy, see Table 1 and Supplementary Table S1 for details) of 2010–2012 summers (July–August). Ambient temperatures were derived from data recorded by thermal sensors embedded in GPS collars fitted on mouflon (Jiang et al. 2012). The letters above 95% CI indicate significant differences in ambient temperatures between habitat types (post hoc Tukey honest significant difference tests).

moorlands situated on plateaux to forested areas situated in slopes (Figure 2). This general pattern was observed in particular during twilight and night, when temperatures on plateaux were significantly lower than in steep rocky areas and forests. During hot and nonwindy days, that is, when the critical temperature threshold controlling mouflon thermoregulation was most probably overrun, rocky areas were clearly the hottest habitat type, whereas plateaux (moorland.p and forest.p) provided more favorable thermal conditions (Figure 2, left panel). However, comparable thermal conditions were revealed during these periods in forested areas whatever their position in slopes or on plateaux.

**Habitat selection at broad scale**

The top model highlighted strong between-sex differences in the selection of summer home ranges (Table 3). Males and females differed in their selection of areas situated on plateaux with females strongly avoiding such habitats compared with males (Figure 3). Irrespective of vegetation cover, the proportion of plateaux in the home ranges of males was on average 1.8 times higher than in the home ranges of females (mean proportions [SD]: males = 37.9 [22.4]%; females = 20.8 [20.1]%). Forested habitats situated on plateaux were in particular included at a higher proportion than available in the study area by males (95% CI higher than 1 for forests on plateaux in males), whereas females avoided them and rather preferred steep rocky areas (Figure 3).

**Habitat selection at fine scale**

SSFs revealed strong variation in habitat selection of both sexes according to weather conditions and day periods (Figure 4). During the day, both sexes avoided plateaux under cool and windy conditions. By contrast, the selection of these areas largely increased under hot and nonwindy days, irrespective of the vegetation cover in males and only for forested areas in females. In addition, both sexes selected forested areas in slopes under these conditions. While

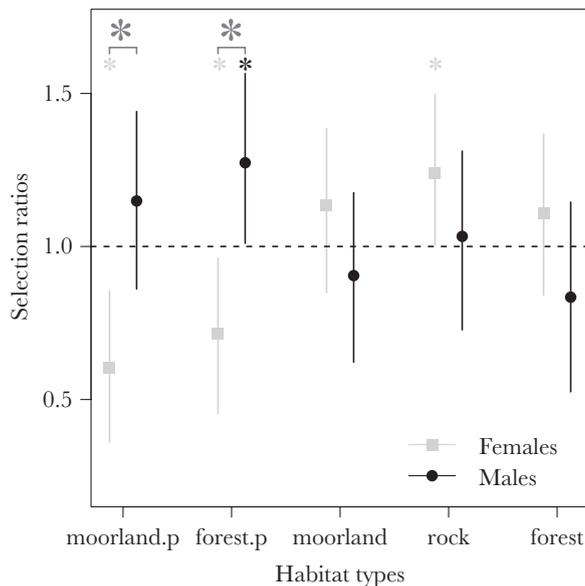
**Table 3**

**Set of models fitted to test for differences in broadscale habitat selection (choices of home range within available landscape, assessed using selection ratios; Manly et al. 2002) between males and females of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) during 2010–2012 summers in the Caroux-Espinouse study area (southern France)**

	<i>k</i>	LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Models					
<b>Habitat × sex</b>	<b>13</b>	<b>-265.33</b>	<b>558.17</b>	<b>0.00</b>	<b>0.91</b>
Null	4	-277.85	563.87	5.70	0.05
Sex	5	-277.47	565.18	7.01	0.03
Habitat	8	-275.33	567.24	9.07	0.01
Habitat + sex	9	-274.94	568.61	10.43	<0.001

These linear mixed-effects models included mouflon identity and year as non-nested grouping factors (random intercept models) to account for repeated measurements on the same individuals and potential between-years differences in selection criteria, respectively. In model acronyms, "+" corresponds to additive effects and "×" to the interaction between the 2 factors. The selected model (lowest AIC<sub>c</sub>) is in bold type. *k* is the number of parameters, LL is the maximum log-likelihood, ΔAIC<sub>c</sub> is the difference in the Akaike information criterion between the selected model and the other ones, and *w<sub>i</sub>* is Akaike weight.

concentrating on moorlands when on plateaux, the selection of forested areas in slopes was also prolonged by males during hot and nonwindy twilights. The habitat selection of females during this period was rather characterized by a strong opposition in decisions concerning the reference habitat type, that is, moorlands in slopes, avoided under hot and nonwindy conditions but selected under cool and windy ones (95% CI of the other habitat types >0 and barely <0, respectively). During the night, variations in habitat selection according to weather conditions were more limited (sex- and habitat-specific 95% CI overlapping whatever the weather conditions). Females that avoided moorlands on plateaux during cool and windy nights did not avoid them during hot and nonwindy



**Figure 3**

Broadscale habitat selection of GPS-collared Mediterranean mouflon females ( $n = 26$ ; gray squares) and males ( $n = 18$ ; black circles) during 2010–2012 summers (July–August) in the Caroux-Espinouse study area (southern France). Selection ratios related the composition of home ranges to the proportions of the different habitat types within the available study area. The coefficients and 95% CI were predicted from the selected model (Table 3). The dashed line represented 1, the reference value indicating when proportions included in home ranges equaled availability in the study area. Selection ratios significantly differing from this reference value, or significantly differing between both sexes, are represented by small and large stars, respectively.

ones. Males that avoided forested areas in slopes during cool and windy nights did not avoid them during hot and nonwindy ones and selected moorlands on plateaux.

### Thermal consequences of habitat selection during the day and temperature thresholds

We found marked threshold-dependent relationships between ambient temperatures derived from sensors embedded in GPS collars of both sexes and reference temperatures recorded at the weather station (Table 4). Below 15.5 °C (females; 95% CI = 13.9–16.5) and 17.1 °C (males; 95% CI = 14.9–19.7) at the weather station, ambient and reference temperatures increased at a close rate (females: 0.94 °C [95% CI = 0.89–0.98] per 1 °C rise at the weather station; males: 0.89 °C [95% CI = 0.85–0.93]), with experienced temperatures on average 1.24 °C [SD = 0.12] higher in females compared with males (Figure 5). The slight average differences between both temperatures (females: 0.44 °C [SD = 0.15]; males: –0.89 °C [SD = 0.32]) during this period when thermal constraints should not be a strong determinant of mouflon habitat selection confirmed the relevance of the records from the weather station and of the method used to derive temperature experienced by mouflon from thermal sensor records.

By contrast, above these temperature thresholds, the increase in ambient temperatures experienced by both sexes was markedly lower than the increase in temperatures at the weather station (females: 0.75 °C [95% CI = 0.73–0.76]; males: 0.77 °C [95% CI = 0.74–0.79]) and also lower than below these thresholds (see

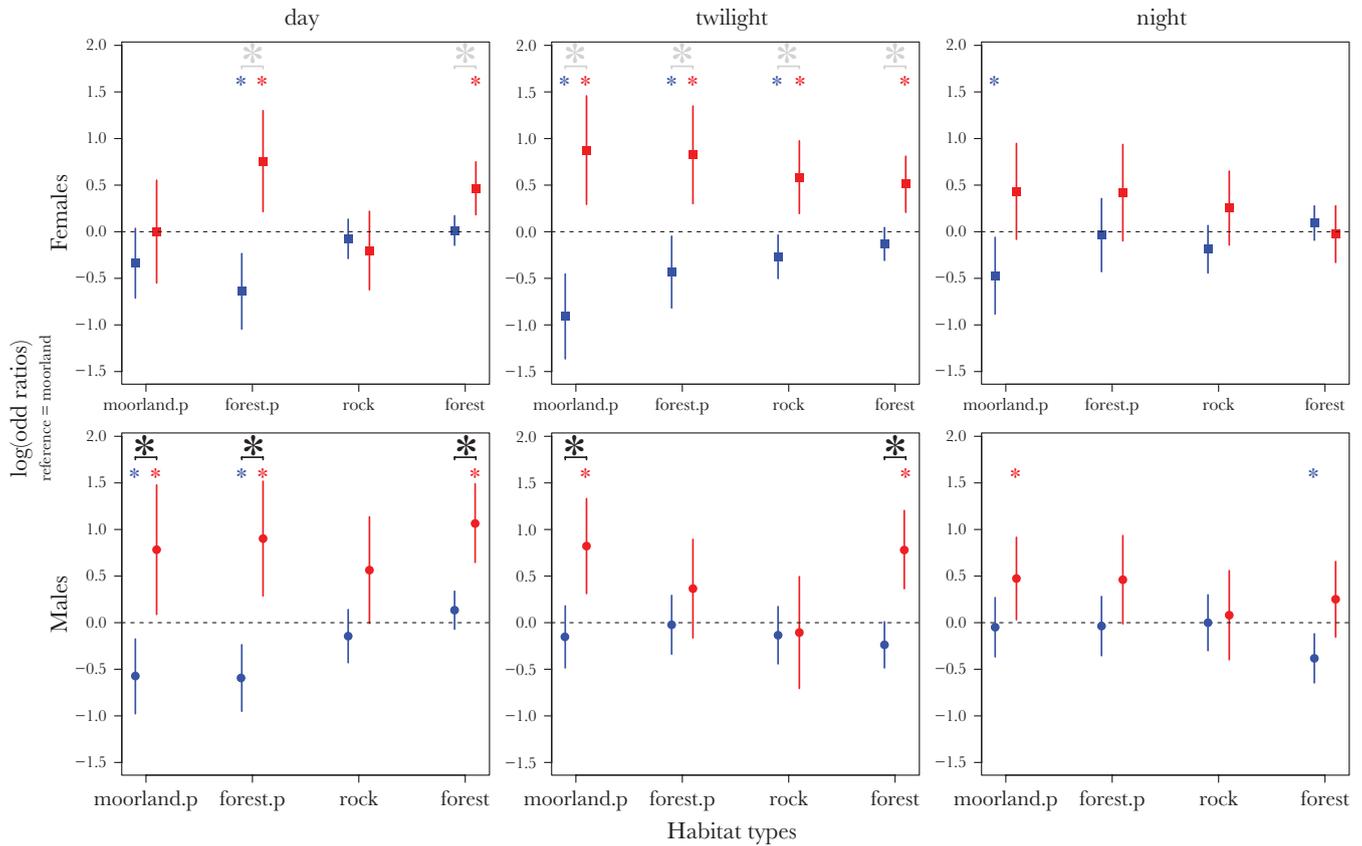
values above). These results showed that both sexes were able to significantly reduce the temperatures they experienced compared with the ones recorded at the weather station. The difference in ambient temperature experienced by both sexes (on average 1.06 °C [SD = 0.08] higher in females compared with males) was maintained.

## DISCUSSION

By analyzing sex- and scale-specific patterns of habitat selection, we were able to determine how males and females of Mediterranean mouflon cope with thermal constraints in addition to the multiple other constraints they experience during summer. Our analyses revealed not only sex-specific criteria for choices of summer home ranges within available landscape but also sex-specific modulations in movement step selection under 2 contrasted weather conditions at the daily scale. The emergence of thermal cover as a main driver of mouflon habitat selection during the day depended on the over-run of temperature thresholds. As a result of these sex-specific criteria of habitat selection, and above these temperature thresholds, average ambient temperatures experienced by mouflon during hot-test day periods increased more slowly than temperatures recorded at the closest weather station and were on average 1.1 °C lower in males than in females.

When choosing a summer home range, females strongly avoided unsafe plateaux and tended to prefer escape terrains in steep rocky areas providing a high visibility while being difficult to reach for potential predators (Hayes et al. 1994; Hamel and Côté 2007). As in other wild sheep (e.g., bighorn sheep *Ovis canadensis*, Festa-Bianchet 1988; Dall sheep *Ovis dalli dalli*, Rachlow and Bowyer 1998; Sardinian mouflon *Ovis orientalis musimon*, Ciuti et al. 2009) and more generally in mountain ungulates (e.g., mountain goats *Oreamnos americanus*, Hamel and Côté 2007), the broadscale habitat selection of females was hence largely driven by conditions that should ensure the survival of their lamb, despite their poor value in terms of thermal cover and foraging conditions (Figure 2; Marchand et al. 2014). By contrast, males that were larger than females included high proportions of the habitat types situated on plateaux in their home ranges, as they provide both high thermal cover and abundant food (42% of moorlands on plateaux were grass-rich pastures, meadows, and cultures devoted to wildlife vs. 4.1% in steep moorlands; Baudière 1970). Although repeatedly proposed as predominant at fine spatial and temporal scales in boreal and mountainous areas (Aublet et al. 2009; van Beest et al. 2012), our results suggested that thermal constraints, influencing males' broadscale habitat selection, could also be one of the most limiting factors for larger individuals in Mediterranean areas.

At finer scale and under cool and windy conditions, both sexes avoided windswept plateaux during the day. Wind increases heat loss, which could improve the thermal balance of ruminants under summer conditions (Silanikove 2000; Cain et al. 2006). However, wind noise and moving vegetation were also suggested to strengthen antipredator behaviors in ungulates (Bowyer and Kie 2009). During hot and nonwindy days, both sexes increased the selection of forests providing the best trade-off between thermal cover and protection from perceived predation risk when mouflon were mostly inactive (Bourgoin et al. 2011). However, males adopted a less secure strategy than lambing females by also selecting moorlands on plateaux, where they gathered during the hottest twilights. Focusing on the habitat type providing the best trade-off between foraging resources and thermal cover during activity peaks may allow males



**Figure 4**

Fine-scale habitat selection of GPS-collared Mediterranean mouflon females ( $n = 26$ ; top panels; squares) and males ( $n = 18$ ; bottom panels; circles) during 2010–2012 summers in the Caroux-Espinouse study area (southern France) according to weather conditions (blue = cool-windy; red = hot-nonwindy; for details, see Table 1 and Supplementary Table S1) and day periods (day = 7–17 h; twilight = 4–6 + 18–20 h; night = 21–3 h UTC). Points represented coefficients provided by sex-specific matched case-control logistic regressions, that is, the log odd ratios for a habitat being chosen relative to a reference habitat for which  $\beta = 0$ , that is, moorland in slopes in our analyses (providing the more explicit graphical representation of the results; represented by the dashed lines). Vertical bars represented 95% CIs derived from robust standard errors (Forester et al. 2009). Small stars indicated coefficients significantly differing from this reference, whereas large stars represented nonoverlapping 95% CI between the 2 weather conditions.

to minimize time spent eating and reduce energetic costs resulting from thermogenic foraging activities under the hottest conditions (time-minimizer strategy sensu Schoener 1971). Females that rather tended to trade-off foraging resources with risk avoidance (i.e., moorlands in slopes) during cool and windy twilights, did not adopt the same strategy as males during hot and nonwindy twilights, and did not delay selection of foraging resources during hottest nights, contrary to our expectations. In a diurnal/crepuscular species (Langbein et al. 1997) for which visibility is important in antipredator behaviors (Hayes et al. 1994; Benoist et al. 2013), foraging during the night may strengthen the food/cover trade-off for lambing females (Beauchamp 2007). This may explain why their shift in activity toward nocturnal hours revealed under hot and nonwindy conditions (Bourgoin et al. 2011) was not concurrent with changes in habitat selection (Figure 4).

Considering sex and time allowed us to reveal the influence of thermal conditions on the fine-scale habitat selection of this dimorphic ruminant species (Bjørneraas et al. 2011; Marchand P, Garel M, Bourgoin G, Dubray D, Maillard D, Loison A, unpublished data). In males, the interplay between daily activity rhythm and habitat selection led to habitat shifts not only during the day, when the thermal threshold controlling thermoregulation was most probably overrun (Maloney et al. 2005), but also

when compensatory responses predicted from activity shifts could occur (Schoener 1971; Bourgoin et al. 2011). In females, however, the response to hot summer conditions was mostly temporal (Bourgoin et al. 2011), spatial responses being restricted to the hottest period at the daily scale. Further research, exploring the importance of body mass on individual scale-specific responses within each sex (Aublet et al. 2009) or comparing patterns in females with different reproductive status (see Pipia et al. 2008 on activity rhythms), may help disentangle the respective influence of the multiple trade-off components in explaining sexual habitat segregation in this species during summer. Indeed, the spatial distribution of resources and conditions in our study area, opposing secure slopes with poor thermal cover and “high” plateaux with opposite characteristics and more abundant food (Figure 1), may reinforce the contrast between sexes in habitat selection. Other hypotheses proposed to explain habitat segregation, that is, sex-specific foraging needs, strategies to ensure reproductive success, and sensitivities to predation risk, may also be at play during this period (Ruckstuhl and Neuhaus 2006).

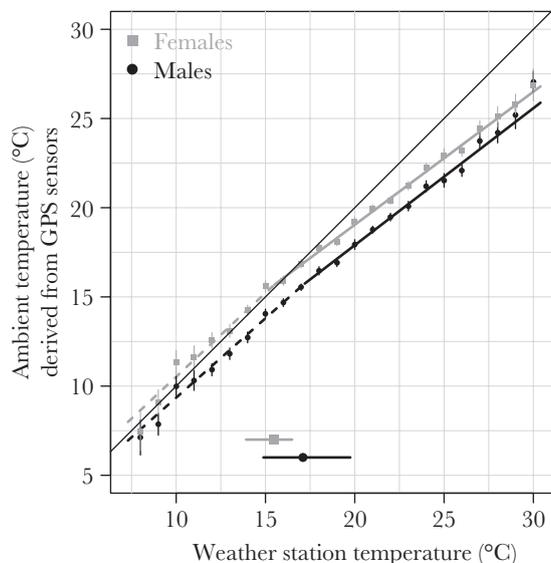
The combined analyses of temperatures recorded in GPS collars and by the weather station revealed that the need for thermal regulation may be a main driver of mouflon habitat selection, but only above a temperature threshold. As commonly reported

**Table 4**

Set of models fitted to investigate the variation in temperatures derived from sensors embedded in GPS collars fitted on Mediterranean mouflon according to temperatures  $T_{ws}$  recorded at the closest weather station (Météo France, Fraïsse-Murat; 1022 m a.s.l., 10 m above the ground, 10 km east from the study area) during 2010–2012 summer days (7–17h UTC) in the Caroux-Espinouse study area (southern France)

	$k$	LL	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
Models					
<b><math>T_{ws} \times \text{sex}</math> (piecewise; sex-specific thresholds)</b>	<b>10</b>	<b>-40750.95</b>	<b>81521.92</b>	<b>0.00</b>	<b>0.85</b>
$T_{ws} + \text{sex}$ (piecewise; 1 threshold for both sexes)	8	-40754.73	81525.47	3.55	0.14
$T_{ws} + \text{sex}$ (nonlinear)	7	-40760.52	81535.04	13.12	<0.01
$T_{ws}$ (piecewise)	7	-40760.81	81535.62	13.70	<0.01
$T_{ws} \times \text{sex}$ (piecewise; 1 threshold for both sexes)	9	-40758.92	81535.85	13.92	<0.01
$T_{ws} \times \text{sex}$ (quadratic)	9	-40760.14	81538.30	16.38	<0.01
$T_{ws} + \text{sex}$ (quadratic)	7	-40762.70	81539.41	17.49	<0.01
$T_{ws} \times \text{sex}$ (nonlinear)	9	-40762.55	81543.12	21.20	<0.01
$T_{ws}$ (nonlinear)	6	-40766.34	81544.68	22.75	<0.01
$T_{ws}$ (quadratic)	6	-40768.77	81549.55	27.63	<0.01
$T_{ws} \times \text{sex}$ (linear)	7	-40782.19	81578.39	56.47	<0.01
$T_{ws} + \text{sex}$ (linear)	6	-40784.45	81580.90	58.98	<0.01
$T_{ws}$ (linear)	5	-40790.50	81591.01	69.08	<0.01
Null	4	-48302.34	96612.69	15090.76	<0.01

These models included mouflon identity and year as non-nested grouping factors (random intercept models) to account for repeated measurements on the same individuals and potential between-year differences in responses, respectively. In model acronyms, "+" corresponds to additive effects and "x" to the interaction between the 2 factors. The selected model (lowest AIC<sub>c</sub>) is in bold type.  $k$  is the number of parameters, LL is the maximum log-likelihood,  $\Delta$ AIC<sub>c</sub> is the difference in the Akaike information criterion between the selected model and the other ones, and  $w_i$  is Akaike weight.

**Figure 5**

Variation in ambient temperatures derived from sensors embedded in GPS collars fitted on Mediterranean mouflon females ( $n = 26$ ; gray squares) and males ( $n = 18$ ; black circles) according to temperatures recorded at the closest weather station (Météo France, Fraïsse-Murat; 1022 m a.s.l., 10 m above the ground, 10 km east from the study area) during 2010–2012 summer days (7–17h UTC) in the Caroux-Espinouse study area (southern France). The relationships (dashed thick lines below the sex-specific thresholds, solid thick lines above) were predicted from the selected model (Table 4). The thin solid line indicated when ambient temperatures derived from sensors equaled temperature recorded at the weather station. Filled points and vertical lines represented the mean and 95% CI of raw ambient temperatures for the corresponding class of weather station temperatures (1 °C classes), respectively. The points and solid horizontal lines at the bottom of the figure represented the thresholds and 95% CI of weather station temperatures beyond which ambient temperatures increased more slowly than temperatures at the weather station (piecewise model, see text for details).

in experimental studies (Maloney et al. 2005; Terrien et al. 2010) and as stated by the heat dissipation limit hypothesis, the maximum capacity of mouflon to dissipate heat was probably reached at/beyond the corresponding ambient temperature experienced by both sexes. Hence, individuals resorted to behavioral thermoregulation to avoid the detrimental effects of hyperthermia (Speakman and Król 2010). This plastic habitat selection contributed to buffer mouflon against the hottest conditions, as found in moose *Alces alces* (e.g., van Beest et al. 2012; Melin et al. 2014), Alpine ibex (Aublet et al. 2009), or North American elk *Cervus elaphus* (Long et al. 2014). Indeed, above the temperature thresholds, the temperatures experienced by both sexes under the hottest day conditions increased at a lower rate than temperatures recorded at the closest weather station. However, though more slowly, ambient temperatures experienced by both sexes never stopped increasing, suggesting that habitat selection might be insufficient to maintain ambient temperatures around the thresholds controlling thermoregulation. Given that the ability and the efficiency of animals to select habitats with required characteristics depended on the availability and quality of these habitats and their surroundings (Ydenberg and Dill 1986; Gill et al. 2001), this result might also suggest a mismatch during summer between the thermal needs of this species and the availability of thermal shelters in this Mediterranean area where mouflon was introduced. However, further assessment of the relative importance of the multiple internal and external factors influencing sensor records (e.g., animal position, activity state and internal temperature, or direct sunlight, but see Materials and Methods) and an experimental evaluation of the critical temperature thresholds controlling thermoregulation are needed to assess more precisely the contribution of habitat selection in buffering mouflon against hot summer conditions (see Long et al. 2014 for an example in North American elk).

Although winter has long been claimed as the critical season for large herbivores in temperate and northern ecosystems, recent studies on the influence of thermal conditions during

summer revealed pervasive consequences on spatial and temporal behaviors of large herbivores from boreal to Mediterranean areas (Aublet et al. 2009; Bowyer and Kie 2009; Bourgoïn et al. 2011; van Beest et al. 2012). Close relationships between fitness components and habitat selection have also been highlighted in large herbivores (McLoughlin et al. 2006 in red deer *C. elaphus*, McLoughlin et al. 2007 in roe deer *Capreolus capreolus*). Furthermore, the presence/absence of phenotypic plasticity has been identified as one of the mechanism by which the effects of climate change on population dynamics arise (see e.g., Charmantier et al. 2008 in birds and Plard et al. 2014 in roe deer). These advances raised questions on the costs of such behavioral responses and on their consequences in terms of energetic balance, fitness, population dynamics, and species persistence (Garel et al. 2004; van Beest and Milner 2013; Long et al. 2014) for Mediterranean mouflon, a species of conservation concerns in Mediterranean areas (Shackleton and IUCN/SSC Caprinae Specialist Group 1997). We revealed that thermal constraints could affect habitat selection of larger individuals at broader scale, suggesting a strong importance for their fitness (Rettie and Messier 2000). In the studied population, previous results revealed a 15.3% decrease in 24-h activity rate of females during hot and nonwindy periods (Bourgoïn et al. 2011). Despite adjustments in habitat selection, our results suggested that these responses could only partially buffer mouflon against the hottest conditions. Females were furthermore constrained not only to forage during the night but also to use foraging habitats that have been found less favorable for individual body mass (open areas in slopes; Marchand et al. 2014). These sex-specific spatiotemporal responses to hot environmental conditions could explain why females were more affected than males during the hottest summers in our population (Garel et al. 2004). Indeed, both adult male and female mouflon harvested after the severe 2003 summer drought were on average 3.4 kg lighter than those harvested during the 3 previous hunting seasons, representing a 11% and 17% body mass loss in males and females, respectively (Garel et al. 2004). It could also explain why lamb survival strongly decreased during heat waves in our study area (Garel et al. 2004) and why female productivity was strongly correlated with a temperature-related parameter (i.e., latitude) in this species (Ciuti et al. 2009). Fully investigating the extent to which individuals are affected by these behavioral responses (see van Beest and Milner 2013 for an example in moose) and the consequences of these latter for population distribution, dynamics, and persistence is hence a crucial step in the context of global warming (Walther et al. 2002; Myrseter and Sæther 2011).

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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## REFERENCES

- Aublet JF, Festa-Bianchet M, Bergero D, Bassano B. 2009. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*. 159:237–247.
- Bates D, Maechler M, Bolker B. 2011. lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-42.
- Baudière A. 1962. Le Parc National du Caroux – essai de synthèse climatique. *Bull Soc Languedoc Géogr*. 33:169–186.
- Baudière A. 1970. Recherches phytogéographiques sur la bordure méridionale du Massif Central français (Les Monts de l’Espinouse) [PhD thesis]. [Montpellier (France)]: Université de Montpellier.
- Beauchamp G. 2007. Exploring the role of vision in social foraging: what happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night? *Biol Rev*. 82:511–525.
- van Beest FM, Milner JM. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS One*. 8:e65972.
- van Beest FM, Van Moorter B, Milner JM. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav*. 84:723–735.
- Belovsky GE. 1981. Optimal activity times and habitat choice of moose. *Oecologia*. 48:22–30.
- Benoist S, Garel M, Cugnasse JM, Blanchard P. 2013. Human disturbances, habitat characteristics and social environment generate sex-specific responses in vigilance of Mediterranean mouflon. *PLoS One*. 8:e82960.
- Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening global positioning system location data for errors using animal movement characteristics. *J Wildl Manage*. 74:1361–1366.
- Bjørneraas K, Solberg EJ, Herfindal I, Moorter BV, Rolandsen CM, Tremblay JP, Skarpe C, Sæther BE, Eriksen R, Astrup R. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildl Biol*. 17:44–54.
- Bourgoïn G, Garel M, Blanchard P, Dubray D, Maillard D, Gaillard JM. 2011. Daily responses of mouflon activity to summer climatic conditions. *Can J Zool*. 89:765–773.
- Bowyer R, Kie JG. 2009. Thermal landscapes and resource selection by black-tailed deer: implications for large herbivores. *Calif Fish Game*. 95:128–139.
- Broders HG, Coombs AB, McCarron JR. 2012. Ecothermic responses of moose (*Alces alces*) to thermoregulatory stress on mainland nova scotia. *Alces*. 48:53–61.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference—a practical information-theoretic approach. 2nd ed. New York: Springer Verlag.
- Cain J, Krausman PR, Rosenstock SS, Turner JC. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. *Wildl Soc Bull*. 34:570–581.
- Calenge C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model*. 197:516–519.
- Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LE, Sheldon BC. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*. 320:800–803.
- Ciuti S, Pipia A, Grignolio S, Ghiandai F, Apollonio M. 2009. Space use, habitat selection and activity patterns of female sardinian mouflon (*Ovis orientalis musimon*) during the lambing season. *Eur J Wildl Res*. 55:589–595.
- Conradt L, Clutton-Brock T, Guinness FE. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Anim Behav*. 59:1049–1060.
- Dwyer CM. 2008. Environment and the sheep. In: Dwyer CM, editor. The welfare of sheep, volume 6 of Animal welfare. Dordrecht (The Netherlands): Springer. p. 41–79.
- Festa-Bianchet M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*. 75:580–586.
- Forester JD, Im HK, Rathouz PJ. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*. 90:3554–3565.
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in yellowstone national park. *Ecology*. 86:1320–1330.
- Garel M, Cugnasse JM, Gaillard JM, Loison A, Gibert P, Douvre P, Dubray D. 2005. Reproductive output of female mouflon (*Ovis gmelini musimon* × *Ovis sp.*): a comparative analysis. *J Zool*. 266:65–71.
- Garel M, Cugnasse JM, Maillard D, Gaillard JM, Hewison AJM, Dubray D. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecol Appl*. 17:1607–1618.

- Garel M, Loison A, Gaillard JM, Cugnasse JM, Maillard D. 2004. The effects of a severe drought on mouflon lamb survival. *Proc R Soc Lond B*. 271:471–473.
- Geist V. 1974. On the relationship of social evolution and ecology in ungulates. *Am Zool*. 14:205–220.
- Gill JA, Norris K, Sutherland WJ. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biol Conserv*. 97:265–268.
- Gillingham MP, Parker KL, Hanley TA. 1997. Forage intake by black-tailed deer in a natural environment: bout dynamics. *Can J Zool*. 75:1118–1128.
- Hamel S, Côté SD. 2007. Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety? *Can J Zool*. 85:933–943.
- Hansen BE. 2000. Sample splitting and threshold estimation. *Econometrica*. 68:575–603.
- Hayes CL, Krausman PR, Wallace MC. 1994. Habitat, visibility, heart rate, and vigilance of bighorn sheep. *Desert Bighorn Council 1994 Trans*. 38:6–11.
- Hopewell L, Rossiter R, Blower E, Leaver L, Goto K. 2005. Grazing and vigilance by Soay sheep on Lundy island: influence of group size, terrain and the distribution of vegetation. *Behav Process*. 70:186–193.
- Hosmer DW, Lemeshow S. 2000. *Applied logistic regression*. New York: Wiley-Interscience, John Wiley & Sons, Inc.
- Huey RB, Tewksbury JJ. 2009. Can behavior douse the fire of climate warming? *Proc Natl Acad Sci USA*. 106:3647–3648.
- Intergovernmental Panel on Climate Change. 2013. *Climate change 2013—the physical science basis—Working Group I contribution to the IPCC fifth assessment report*. New York: Cambridge University Press.
- IUPS Thermal Commission. 2001. Glossary of terms for thermal physiology. *Jpn J Physiol*. 51:2001.
- Jiang Z-W, Takatsuki S, Kitahara M, Sugita M. 2012. Designs to reduce the effect of body heat on temperature sensor in board house of gps radio-collar. *Mammal Study*. 37:165–171.
- Jiguet F, Julliard R, Thomas CD, Dehorter O, Newson SE, Couvet D. 2006. Thermal range predicts bird population resilience to extreme high temperatures. *Ecol Lett*. 9:1321–1330.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos*. 69:373–386.
- Langbein J, Scheibe KM, Eichhorn K. 1997. Seasonal changes in the circadian behaviour patterns in European mouflons (*Ovis ammon musimon* Pallas, 1811). *Zeitschr Saeugetierkunde*. 62:117–123.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool*. 68:619–640.
- Long RA, Bowyer RT, Porter WP, Mathewson P, Monteith KL, Kie JG. 2014. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol Monogr*. 84:513–532.
- Maloney SK, Moss G, Cartmell T, Mitchell D. 2005. Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *J Comp Physiol A Neuroethol Sens Neural Behav Physiol*. 191:1055–1064.
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Dordrecht (The Netherlands): Kluwer Academic Publisher.
- Marchand P, Garel M, Bourgoin G, Michel P, Maillard D, Loison A. 2014. Habitat-related variation in carcass mass of a large herbivore revealed by combining hunting and gps data. *J Wildl Manage*. 78:657–670.
- Marchand P, Redjadj C, Garel M, Cugnasse JM, Maillard D, Loison A. 2013. Are mouflon (*Ovis gmelini musimon*) really grazers? A review of variation in the composition of their diet. *Mammal Rev*. 43:275–291.
- McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc R Soc B Biol Sci*. 273:1449–1454.
- McLoughlin PD, Gaillard JM, Boyce MS, Bonenfant C, Messier F, Duncan P, Delorme D, Van Moorter B, Saïd S, Klein F. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*. 88:3192–3201.
- Melin M, Matala J, Mehtätalo L, Tiilikainen R, Tikkanen OP, Maltamo M, Puseenius J, Packalen P. 2014. Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests—an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biol*. 20:1115–1125.
- Mysterud A, Ostbye E. 1999. Cover as a habitat element for temperate ungulates. *Wildl Soc Bull*. 272:385–394.
- Mysterud A, Sæther BE. 2011. Climate change and implications for the future distribution and management of ungulates in Europe. In: Putman R, Apollonio M, Andersen R, editors. *Ungulate management in Europe: problems and practices*. Cambridge (UK): Cambridge University Press. p. 349–375.
- Owen-Smith N. 1998. How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *J Zool*. 246:183–192.
- Pippa A, Ciuti S, Grignolio S, Luchetti S, Madau R, Apollonio M. 2008. Influence of sex, season, temperature and reproductive status on daily activity patterns in sardinian mouflon (*Ovis orientalis musimon*). *Behaviour*. 145:1723–1745.
- Plard F, Gaillard JM, Coulson T, Hewison AJ, Delorme D, Warnant C, Bonenfant C. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biol*. 12:e1001828.
- Porter WP, Kearney M. 2009. Size, shape, and the thermal niche of endotherms. *Proc Natl Acad Sci USA*. 106(Suppl 2):19666–19672.
- R Development Core Team. 2013. *R: a language and environment for statistical computing*. Vienna (Austria): R Foundation for Statistical Computing.
- Rachlow JL, Bowyer RT. 1998. Habitat selection by dall's sheep (*Ovis dalli*): maternal trade-offs. *J Zool*. 245:457–465.
- Rettie WJ, Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*. 23:466–478.
- Risenhoover KL, Bailey JA. 1985. Foraging ecology of mountain sheep: implications for habitat management. *J Wildl Manage*. 49:797–804.
- Roever CL, Boyce MS, Stenhouse GB. 2010. Grizzly bear movements relative to roads: application of step selection functions. *Ecography*. 33:1113–1122.
- Rubin ES, Bleich VC. 2006. Sexual segregation: a necessary consideration in wildlife conservation. In: Ruckstuhl K, Neuhaus P, editors. *Sexual segregation in vertebrates—ecology of the two sexes*. Cambridge (UK): Cambridge University Press. p. 379–391.
- Ruckstuhl KE, Neuhaus P, editors. 2006. *Sexual segregation in vertebrates—ecology of the two sexes*. Cambridge (UK): Cambridge University Press.
- Sæther B-E, Sutherland WJ, Engen S. 2004. Climate influences on avian population dynamics. *Adv Ecol Res*. 35:185–209.
- Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. 2014. Microhabitats reduce animal's exposure to climate extremes. *Global Change Biol*. 20:495–503.
- Schoener TW. 1971. Theory of feeding strategies. *Annu Rev Ecol Syst*. 2:369–404.
- Shackleton DM, IUCN/SSC Caprinae Specialist Group. 1997. *Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae*. Gland (Switzerland): IUCN.
- Shrestha AK, van Wieren SE, van Langevelde F, Fuller A, Hetem RS, Meyer L, de Bie S, Prins HH. 2014. Larger antelopes are sensitive to heat stress throughout all seasons but smaller antelopes only during summer in an African semi-arid environment. *Int J Biometeorol*. 58:41–49.
- Silanikove N. 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. *Livest Prod Sci*. 67:1–18.
- Singh NJ, Bonenfant C, Yoccoz NG, Côté SD. 2010. Sexual segregation in Eurasian wild sheep. *Behav Ecol*. 21:410–418.
- Speakman JR, Król E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *J Anim Ecol*. 79:726–746.
- Terrien J, Perret M, Aujard F. 2010. Behavioral thermoregulation in mammals: a review. *Front Biosci*. 16:1428–1444.
- Therneau T. 2013. *A package for survival analysis in S*. R package version 2.37-4.
- Thurfjell H, Ciuti S, Boyce MS. 2014. Applications of step-selection functions in ecology and conservation. *Movem Ecol*. 2:4.
- Tronchet M. 2008. *Cartographie des habitats du massif du Caroux-Espinouse (Hérault) à partir de photos aériennes de 2005*. Technical report. Groupement d'Intérêt Environnemental et Cynégétique du Caroux-Espinouse – Office National de la Chasse et de la Faune Sauvage, Castanet-le-Haut.
- Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced environmental change. *Biol Rev*. 86:640–657.
- Wakelyn L. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. *J Wildl Manage*. 51:904–912.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature*. 416:389–395.
- Weladji RB, Klein DR, Holand Ø, Mysterud A. 2002. Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer*. 22:33–50.
- Wood SN. 2006. *Generalized additive models: an introduction with R*. Boca Raton (FL): Chapman & Hall/CRC Press.
- Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*. 70:164–168.
- Ydenberg RC, Dill LM. 1986. The economics of fleeing from predators. *Adv Stud Behav*. 16:229–249.