



# Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area



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## ABSTRACT

Human disturbance is of growing concern owing to the increase of human activities in natural areas. Animal responses are manifold (immediate and/or delayed, short and/or long-lasting, with numerous behaviors affected) so that comprehensive studies are few. Here, we contrasted days with low or high tourism or hunting pressures to assess direct (daytime) and indirect (nighttime) responses of 66 GPS-collared Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. from the Caroux-Espinouse massif (southern France) in terms of movement, habitat use and daily activity. We took advantage of the fact that both human activities occurred during different periods and with different intensities in 3 contiguous areas (among which a protected area without hunting and with limited tourism) to compare their influence on mouflon behavior. Mouflon response to tourism was limited to the area where tourism pressure was intense with a decrease in diurnal activity compensated during nighttime by an increase of nocturnal activity. Hunting had marked consequences in the two hunted areas, with a similar shift in activity between day and night, a decrease in movement sinuosity during daytime by females and an increase in nocturnal use of the best foraging habitats by males, all suggesting an increase in foraging activities during nights following disturbance. The diurnal activity of mouflon living in the protected area was also modified during hunting period, but without nocturnal compensation. These findings revealed that the impact of hunting was higher than tourism, with several components of animal behavior affected. This calls for further research on hunting side-effects in terms of disturbance, especially as it occurs during both the adverse climatic season and the breeding period.

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## 1. Introduction

Human impact on wildlife is a major topic of interest owing to the colossal range of influence of human activities, e.g. on climate, species distribution, habitat structure or ecosystems functioning (Vitousek et al., 1997; Levinsky et al., 2007). In addition to these well-known consequences of human activities, less obvious but pervasive effects have been highlighted (Palumbi, 2001). Among them, the impact of disturbance on animals behavior in the short term, and further, on wildlife populations and communities in

the long term (Liddle, 1997; Lusseau and Bejder, 2007), is now recognized as a crucial issue owing to the development and diversification of human activities in natural areas during the last decades (Flather and Cordell, 1995; Reynolds and Braithwaite, 2001). Indeed, these human-induced behavioral disruptions generally divert time and energy from other fitness-enhancing activities, can elevate energetic costs (e.g. Bélanger and Bédard, 1990 in birds, Williams et al., 2006 in marine mammals), with potential consequences on individuals immune response and health (e.g. Amo et al., 2006; French et al., 2010 in reptiles) or reproductive success (e.g. Phillips and Alldredge, 2000; French et al., 2011 in several mammals). Ultimately intra- (e.g. Fox and Madsen, 1997 in birds, Jedrzejewski et al., 2006 in ungulates) and inter-specific relationships (e.g. predator–prey relationships in large mammals, Muhly et al., 2011) can also be affected by human activities.

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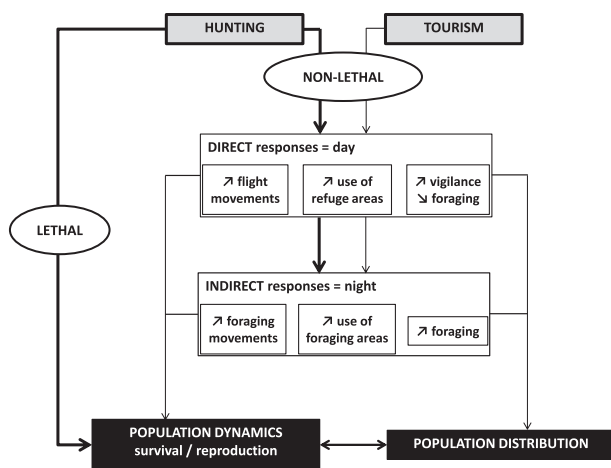
Humans have long been predators of wild animals (lethal impact, Fig. 1), allowing to extend the theoretical background from predator–prey relationships to human-wildlife interactions (Frid and Dill, 2002). Whether humans pose lethal threat to animals or not (Fig. 1), they can still be perceived as predators. For instance, the detrimental effects of hunting on animals behavior have been documented in several groups (birds: Bélanger and Bédard, 1995; mammals: Tolon et al., 2009; Saïd et al., 2012) and in both target and non-target species (Grignolio et al., 2011). Animals may respond to spatial and temporal variations in human activities (Brown et al., 1999; Lima and Bednekoff, 1999; Laundré et al., 2001; Ferrari et al., 2009), attempting to balance decisions concerning risk of encountering humans with those concerning other fitness-enhancing behaviors (optimization trade-offs; Lima and Dill, 1990; Lima, 1998). The immediate responses when risk is perceived as high (hereafter called direct responses, Fig. 1), can be to decrease activity rates (Kaczensky et al., 2006; Podgórski et al., 2013), to display a quick flight for escaping the source of risk (with consequences on movement characteristics, e.g. Sunde et al., 2009; Sibbald et al., 2011; Thurffjell et al., 2013) and/or to use safer areas (Sunde et al., 2009; Tolon et al., 2009; Saïd et al., 2012). However, responses can also be more complex and continue after risk has disappeared, in particular when direct responses include spatial disruptions (e.g. Sunde et al., 2009). Indeed, as predicted from the risk allocation hypothesis (Lima and Bednekoff, 1999), animals could display indirect responses to compensate for energy expenditure or lost foraging opportunities (hereafter called indirect responses, Fig. 1; Bélanger and Bédard, 1990; Riddington et al., 1996). A higher nocturnal activity was found in animals experiencing intense diurnal human activities (George and Crooks, 2006; Naylor et al., 2009; Ohashi et al., 2013). Unfortunately, the possibility of compensatory behaviors has rarely been disclosed in empirical analyses (Tolon et al., 2009), as it is more of a challenge to grasp animal nocturnal behaviors and as most studies focused on a unique direct response to experimental disturbance stimuli (e.g. flight distance, vigilance behavior). Owing to the recent advances in GPS technology and embarked bio-loggers, it is now possible to obtain more accurate information on both short-term and compensatory responses to human disturbance. In addition, combining data recorded concurrently by these devices could help to better grasp the whole consequences of human activities in

terms of foraging behavior (Van Moorter et al., 2010; Owen-Smith et al., 2012).

Since large predators have approached extinction in most of Europe (Breitenmoser, 1998), the system changed to a single “predator” for numerous harvested species, isolating the role of human activities in behavioral strategies observed in wildlife. However, different behavioral responses could occur in harvested species faced with their single “predator” during hunting period, or with a “predation-free predator”, during the rest of the year (Beale and Monaghan, 2004). When disturbance is high and actual risk is low (e.g. with recreationists, who have no direct effects on animals survival), habituation could dampen the intensity of the responses to disturbance. Numerous protected areas have been created to precisely prevent animals from humans and hunting drawbacks in particular (Eagles and McCool, 2002). But they also exacerbate non-consumptive recreational activities, with possible detrimental effects of disturbance on animal behavior (Stockwell et al., 1991; George and Crooks, 2006; Guillemain et al., 2007). “Non-habituated” animals from protected areas could respond more intensively and/or at a lower level of exposure to humans than individuals facing regular disturbance stimuli in unprotected ones. Despite a renewed interest in the consequences of hunting and recreational activities for wildlife (Neumann et al., 2010; Grignolio et al., 2011; Thurffjell et al., 2013), the issues of context-dependent decisions made by animals, e.g. according to the nature and the level of exposure to human activities, in both protected and unprotected areas, still remain largely unexplored (Knight and Cole, 1995; Beale, 2007).

We evaluated the relative effects of hunting and tourism on Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) focusing on 3 behavioral metrics related to the foraging and spatial behaviors of large herbivores, and possibly influenced by risk and disturbance: (1) movement sinuosity (i.e. an index combining step length and turning angles), (2) habitat use, and (3) activity pattern. We obtained detailed data on location and activities year- and day-round owing to GPS collars with activity loggers, fitted on 66 individuals (18 males, 48 females). We relied on 4 marked contrasts to assess the relative responses of mouflon to hunting and touristic activities: (1) a protected versus 2 hunted areas, (2) 2 areas where touristic pressure was low (among which the protected area) versus 1 where it was high, (3) touristic versus hunting periods, in particular in the area where both human activities occurred, (4) days with low and high disturbance (Mondays and Sundays, respectively) in the area(s) where intense human activities occurred. By comparing Sundays and Mondays across all modalities of our disturbance variables, our study design offers a unique opportunity to assess the context-dependent direct and indirect behavioral responses of mouflon to the effects of tourism and hunting.

Our predictions concerning the amount and the direction of responses expected from animals experiencing high tourism and/or hunting pressures are detailed in Fig. 1. As direct responses of Mediterranean mouflon during disturbed days (Fig. 1), we hence expected less sinuous movements (i.e. longer and straighter flight/non foraging movements; Sunde et al., 2009; Van Moorter et al., 2010; Sibbald et al., 2011), increased use of forests and steep slopes (i.e. refuge areas in our study area), reduced use of flat areas and moorlands (i.e. unsafe and foraging areas in our study area; e.g. Grignolio et al., 2011; Saïd et al., 2012), and/or reduced activity rates (e.g. George and Crooks, 2006; Ohashi et al., 2013). As indirect responses during nights following disturbance (Fig. 1), we expected more sinuous movements, increased use of flat moorlands, reduced use of steep slopes and forests, and/or increased activity rates resulting from the increase in foraging activities. We also expected lowest responses of mouflon during the touristic period compared with the hunting period in the area where both



**Fig. 1.** Predictions concerning the direction of both direct and indirect behavioral responses expected from animals experiencing high tourism and/or hunting pressures. The theoretical framework and examples on which these predictions have been built are provided in Section 1. Larger arrows were used to represent hunting non-lethal effects as more pronounced responses were expected to hunting compared with tourism.

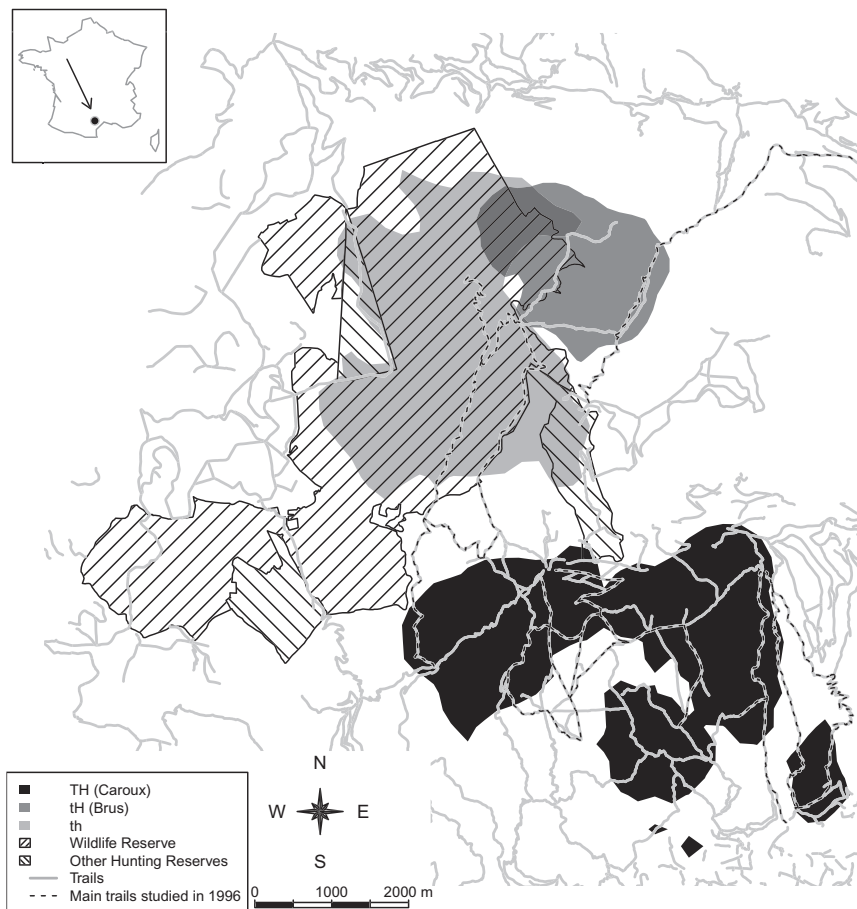
human activities occurred intensively. Finally, we investigated the occurrence of behavioral responses in individuals from the protected area despite the low level of human pressures.

## 2. Materials and methods

### 2.1. Study site and population

Data were collected during 2003–2012 in the Mediterranean mouflon population inhabiting the Caroux-Espinouse massif (southern France; 43°38'N, 2°58'E, 17 000 ha, 150–1 124 m a.s.l.; Fig. 2; see Garel et al., 2005 for more details on the population). Three areas with contrasted situations regarding human activities were distinguished (Fig. 2, Table 1A and B). In a central protected area (Wildlife Reserve and three adjacent hunting reserves), hunting was forbidden and recreational activities were restricted to hiking on few main trails (hereafter called “th”, with  $t$  = low tourism pressure and  $h$  = low hunting pressure). In surrounding unprotected areas, high hunting pressure occurred during daytime from 1st of September to the end of February. Two of these unprotected areas, characterized by marked spatio-temporal variation in recreational activities (Martinetto et al., 1998), were studied (Brus = “tH” and Caroux = “TH”, with  $T$  = high tourism pressure

and  $H$  = high hunting pressure; Fig. 2, and Table 1A and B). Hunting was the main source of regulation for this population since large predators are absent (on average  $393 \pm 111$  animals harvested per year). Driven hunts with hounds was the method used on Wednesdays, Saturdays, Sundays and public holidays (target species being mainly wild boar *Sus scrofa scrofa* but also mouflon and some roe deer *Capreolus capreolus*). Only mouflon were stalked on the other week days (maximum of 4 hunting guides each accompanying one or two hunters in the whole harvesting area). Small game hunting was assumed to be negligible. Recreational activities, generally consisting of hiking (>92% of tourists were hikers; Martinetto, 1995), also displayed contrasted spatio-temporal patterns (Maublanc et al., 1992; Martinetto et al., 1998). Martinetto et al. (1998) showed that the number of hiker groups during March–August was higher in TH than in th and tH areas, and higher on Sundays than on weekdays (for a summary and details on human activities in these 3 areas, see Table 1A and Appendix A, respectively). Given that the increase in touristic pressure between weekdays and Sundays was similar in the 3 areas (nearly  $\times 2$ ), the differences in behavioral responses observed between the 3 areas could be related to variation in tourism intensity rather than to inconsistent variation in the difference between Sundays and weekdays in the 3 areas. In addition, the touristic pressure was mostly concentrated on March–October period



**Fig. 2.** Areas occupied by the 66 GPS-collared mouflon (18 males, 48 females) studied between 2003 and 2012 in 3 areas of the Caroux-Espinouse massif ( $n_{th} = 24$ ,  $n_{tH} = 19$ ,  $n_{TH} = 23$ ; for details, see Table 1). The acronyms of the 3 studied areas were derived from the combination of “ $t$ ” = low tourism pressure, “ $T$ ” = high tourism pressure, “ $h$ ” = low hunting pressure, “ $H$ ” = high hunting pressure (see Table 1A and Appendix A for details; real names between brackets in the legend). Light gray lines represented trails where hiking was allowed. The shaded polygons represented the areas where hunting was forbidden (Wildlife Reserve + 3 other hunting reserves) and where the other human activities were restricted to hiking on identified trails (Wildlife Reserve only). The large overlap between the range used by mouflon from tH and th areas was mostly explained by the selection of a plateau included in the Wildlife Reserve providing favorable foraging conditions during touristic period by rams (56% of rams locations in the Wildlife Reserve during March–September period versus 11% for ewes). During hunting period, the conditions regarding Wildlife Reserve protection largely differed between animals from tH and th areas (22% and 4% of rams’ and ewes’ locations inside the Wildlife Reserve versus 98% and 91%, respectively).

**Table 1**  
(A) Description of human activities, (B) habitat characteristics in the 3 studied areas, (C) number of GPS-collared individuals and (D) number of 48 h periods analyzed to investigate behavioral consequences of tourism and hunting in Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis sp.*) from the Caroux-Espinouse massif (southern France) between 2003 and 2012.

		th (1390 ha)		tH (617 ha)		TH (1448 ha)							
<i>(A) Human activities</i>													
Tourism (March–August)	Intensity	1.6		1		5.1							
	Sunday versus weekday	×2.3		×1.8		×2.4							
Hunting (September–February)	Occurrence	No		Yes		Yes							
	Sunday versus weekday			Driven hunt with hounds versus stalking (both areas)									
<i>(B) Habitat proportions (%)</i>													
Forest		47.3		61.1		48.0							
Slope > 30°		23.7		37.2		32.8							
Moorland		21.6		8.9		20.9							
Slope < 10°		27.9		11.5		20.3							
<i>(C) Number of GPS-collared individuals</i>													
Recording procedure A (20 min)		M	F	M	F	M	F						
		0	1	6	11	4	16						
Recording procedure B (2 h)		7	16	0	2	1	2						
<i>(D) Number of 48 h periods analyzed</i>													
		M	F	M	F	M	F						
		TP	HP	TP	HP	TP	HP						
Movement characteristics	2 h	116	139	269	293	79	52	137	115	75	49	160	110
	20 min	/	/	18	12	88	62	148	120	71	45	162	105
Habitat use		/	/	/	/	87	61	143	120	71	42	162	105
Activity pattern		136	151	229	239	66	47	79	54	83	56	191	133

The acronyms of the 3 studied areas were derived from the combination of “t” = low tourism pressure, “T” = high tourism pressure, “h” = low hunting pressure, “H” = high hunting pressure. Data on tourism pressure comes from [Martinetto et al. \(1998\)](#) with tH data as a reference for intensity (see also [Appendix A](#) for details). Proportions of each habitat type were computed within the 99% kernel range of the locations of all the individuals assigned to a specific site (areas given between brackets and represented in [Fig. 2](#)). TP = touristic period (March–August), HP = hunting period (September–February), M = Males, F = Females. When analyzing movement sinuosity at the 2 h scale, 20 min GPS data were resampled to standardize the time interval between data (2 h) and included in this analysis.

(>200 000 tourists; [Dérioz and Grillo, 2006](#)) and did not seasonally fluctuate during this period ([Martinetto et al., 1998](#)). Tourism was more limited during November–February period as facilities were closed and recreational activities of local people ( $\approx 4\ 800$  inhabitants over  $\approx 17\ 000$  ha) were frequently constrained by adverse climatic conditions during this period of the year ([Baudière, 1962](#)). Tourism occurred during September and October (with the same spatial contrasts as during March–August) but largely dropped on weekdays so that the overall weekly touristic pressure was lower during this period than during the March–August period ([Martinetto et al., 1998](#)). Preliminary analysis did not reveal specific responses during this period compared with the rest of the hunting period (November–February; results not shown). We hence contrasted touristic period (March–August, i.e. tourism only) versus hunting period (September–February). Finally, comparing behavioral responses observed in tH and TH during touristic period should provide information on the influence of high tourism pressure whereas the contrast between th and TH during hunting period should reveal the influence of high hunting pressure.

## 2.2. GPS locations and head motions sensors

We used data collected from 18 adult males and 48 adult females ( $\geq 3$  years old) trapped during the springs of 2003–2012 and fitted with Lotek GPS collars 3300S (revision 2; Lotek Engineering Inc., Carp, Ontario, Canada). All the animals were treated according to the ethical conditions detailed in the specific accreditations delivered to the Office National de la Chasse et de la Faune Sauvage 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).

Each GPS-collared mouflon was assigned to 1 of the 3 studied areas (th, tH or TH; [Fig. 2](#) and [Table 1](#)) according to knowledge on spatial structures in this population. Previous studies revealed matching spatial and genetic structures, suggesting the existence

of several spatially segregated sub-populations ([Petit et al., 1997](#); [Martins et al., 2002](#)). In addition, movements of GPS-collared animals confirmed the absence of movements between TH and the other study areas and the limited exchanges between th and tH (<12% of locations from one of these areas were in the range occupied by the other; [Fig. 2](#)). GPS collars deployed from 2003 to 2009 recorded locations every 20 min during 48 h periods, from Sunday (or public holiday; hereafter called “Sunday”, i.e. day with intense human activities during daylight in the corresponding areas) at 3 h UTC to Tuesday (or public holiday + 2 days; hereafter called “Monday”, i.e. day with low level of human activities) at 2 h UTC, 1 to 4 times per month during battery life (144 locations per 48 h; recording procedure A; [Table 1](#)). GPS collars deployed from 2010 to 2012 recorded locations alternating between even hours on one day and odd hours on the other day, every day during battery life (12 locations per day; recording procedure B; [Table 1](#)).

All GPS collars included 2 perpendicular captive-ball tilt switches (X and Y motion sensors) continuously recording head motions for each 5 min period during battery life. The X motion sensor recorded side to side head motions while Y sensor recorded forward–backward motions and the proportion of time the animal was head down (HD) for each 5 min period (for more details, see [Bourgoin et al., 2008, 2011](#)).

## 2.3. Study design

In order to assess the potential disturbance (i.e. deviation in an animal's behavior from patterns occurring without human influences; [Frid and Dill, 2002](#)), we computed the difference between behavioral responses computed on Sunday and on Monday for each 48 h period and for each mouflon (see metrics used to quantify behavioral responses in [Section 2.4](#) below). When testing for day- and night-specific responses, we computed and contrasted the difference between day with high and day with low level of human activities, with the night following high and night following



low level of human activities. Each 48 h period was divided in the 4 corresponding periods according to civil twilight provided by the Institut de Mécanique Céleste et de calcul des Ephémérides (<http://www.imcce.fr>; for details, see Bourgoïn et al., 2011). By analyzing differences between consecutive days differing by their level of disturbance, rather than using raw values, we aimed at controlling for confounding effects that could influence the behavioral metrics studied (e.g. climatic seasonality, animal physiological state; Bourgoïn et al., 2011; Basille et al., 2012).

#### 2.4. Behavioral metrics

##### 2.4.1. Movement sinuosity

We first analyzed disturbance-related differences in movement sinuosity *SI*. This metric combines step length and turning angle and provides crucial information on the foraging activity of large herbivores (Van Moorter et al., 2010; Owen-Smith et al., 2012). It was computed as  $SI = 2 \left[ p \left( \frac{1-c^2-s^2}{(1-c)^2+s^2} \right) + b^2 \right]^{-0.5}$ , where  $p$  = mean step length,  $c$  = mean cosine of turning angle,  $s$  = mean sine of turning angle,  $b$  = coefficient of variation of step length over the period considered (Benhamou, 2004). We calculated *SI* by day and night (scale = 20 min; only in tH and TH areas) or for the whole day (scale = 2 h, in the 3 areas). In this latter case, 20 min GPS data were resampled to standardize the time interval between data (2 h) and included in the analysis.

We selected trajectories beginning at 2 h UTC (days with even hours in procedure B) or 3 h UTC (procedure A and days with odd hours in procedure B) on Sundays (or public holiday) and ending at 22 h UTC (days with even hours in procedure B) or 23 h UTC (procedure A and days with odd hours in procedure B) on Mondays (or public holiday + 1) with intervals of 2 h. Hence, for each day in a specific 48 h period, 11 location records with 2 h intervals were scheduled. Only 48 h periods for which the number of missing values (due to location failure) did not exceeded 2 for both days were analyzed (Table 1). Because only 1 GPS collar with recording procedure A was used in th, we restricted our analyses on tH and TH when investigating 20 min movements sinuosity, and likewise only analyzed 48 h periods with less than 15 missing locations (Table 1).

##### 2.4.2. Habitat use

We restricted our analyses to tH and TH where recording procedure A provided enough data for habitat use analysis. The disturbance-related differences in the proportions of locations in safe areas, i.e. forests or slope >30°, and less safe and/or more favorable for foraging, i.e. slope <10° and moorlands (see Garel et al., 2007 for a classification; Baudière, 1970; Marchand et al., 2014) were computed for day and night periods. Vegetation characteristics were derived from the processing (K-means unsupervised classification) of a SPOT satellite image taken in July 2005 and field validation in a 25 m × 25 m grid (Tronchet, 2008). Each pixel was characterized by the dominant habitat type. Slope classes were derived from a digital elevation model (source: BD ALTI® dataset of the Institut Géographique National).

##### 2.4.3. Activity pattern

We applied a discriminant model based on calibration with direct observations of free-ranging mouflon to identify active and inactive 5 min bouts from values recorded by motion sensors (active = travelling, feeding, standing or other activities; inactive = lying, resting, sleeping or ruminating; for more details, see Bourgoïn et al., 2008, 2011). We then computed the differences

in proportions of time each individual was active per hour (pA), previously derived from 5 min activity data.

#### 2.5. Statistical analyses

We used linear mixed effect models (LMMs; Pinheiro and Bates, 2000) to assess responses in movement sinuosity and habitat use to human stimuli. Mouflon identity and 48 h period were used as grouping factors to account for repeated measures (several 48 h periods for each individual and several individuals for each 48 h period). Since tourism and hunting could induce site-specific patterns of disturbance, data from March–August (hereafter called “touristic period”) and September–February (hereafter called “hunting period”) were analyzed separately. We considered site as a 3 levels factor, contrasting all studied areas, or as a 2 levels factor combining site of similar level of human activities during a specific period (e.g.  $t$  versus  $T$  during touristic period; see Tables 1A and 2). We also included a sex effect as sex-specific responses to disturbance stimuli could occur in this dimorphic species as a consequence of habitat and social segregation (Le Pendu et al., 1995; Cransac and Hewison, 1997). Finally, a day/night factor (only for scale = 20 min), as well as all interactions among factors, were also included in analyses.

General Additive Mixed Models (GAMMs) including the factors previously described (except day/night since analyses were conducted at a hourly scale) were used to test and represent daily variations in activity patterns between both days for each disturbance source according to site and sex. A cubic regression spline allowed models to account for cyclic variations at the daily scale. A linear relationship was indicated by an estimated degree of freedom (edf) of 1 whereas non-linear relationships corresponded to edf >1 (Wood, 2006).

Model ordering (LMMs and GAMMs) was performed using Akaike's Information Criterion with second order adjustment ( $AIC_c$ ) to correct for small-sample bias; Burnham and Anderson, 2002). Models with  $\Delta AIC_c < 2$  were considered to be equally supported by the data. Hence, model-averaged parameters derived from the set of models with  $\Delta AIC_c < 2$  were then represented to account for model selection uncertainty (Burnham and Anderson, 2002). Behavioral responses were considered as significantly affected by human activities when the 95% confidence interval (95% CI) of the estimated value of its difference did not include 0. We performed all statistical analyses using R 3.0.2 (R Development Core Team, 2013) and adehabitatMA, adehabitatLT, lme4, mgcv and MuMIn libraries for maps and trajectories' characteristics computing, LMMs, GAMMs and model-averaging procedure, respectively (Calenge, 2006; Wood, 2006; Bates et al., 2011).

### 3. Results

#### 3.1. Movement sinuosity

During the touristic period, the sinuosity of movements did not differ between disturbed and undisturbed days, regardless of temporal scale, sex or study area, and despite the contrasted touristic pressure in the 3 areas (null models selected, Table 2 and 95% confidence intervals of models predictions including 0, Fig. 3). By contrast, sinuosity differed according to human pressure during hunting period at both the 2 h and 20 min scales (Table 2 and Fig. 3). Whereas differences in 2 h movements sinuosity did not differ from 0 in th, less sinuous movements were found in both harvested areas during the disturbed day than during the undisturbed day (tH and TH; Table 2 and Fig. 3). At a finer scale, in both hunted areas, movements sinuosity in females tended to decrease

**Table 2**  
Model selection tables investigating (A) tourism and (B) hunting disturbance on movements sinuosity (scales = 2 h and 20 min), habitat use and activity patterns of 66 GPS-collared Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) living in the Caroux-Espinouse massif (southern France), between 2003 and 2012.

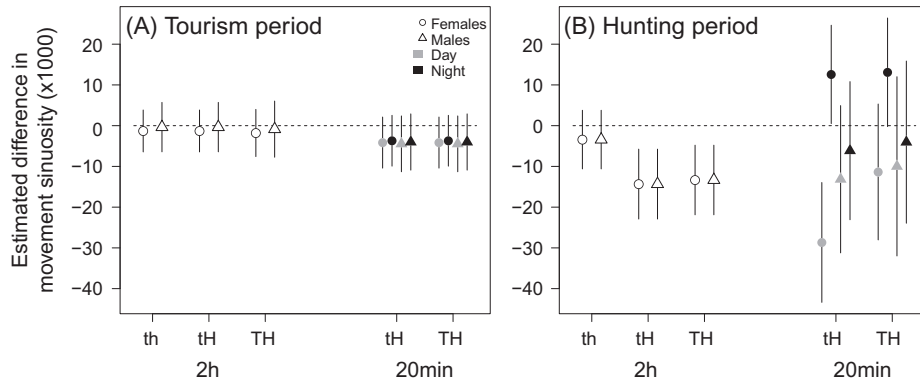
		Models	K	$\Delta AIC_c$	$AIC_c w$	
<i>(A) Touristic period</i>						
Movement sinuosity	2 h	null	4	0	0.41	
		sex	5	1.40	0.20	
		disturb	5	1.79	0.17	
	20 min	null	4	0.00	0.29	
		day/night	5	1.85	0.12	
		sex	5	1.95	0.11	
	Habitat use	Forest	null	4	0	0.22
			sex	5	0.96	0.14
			sites <sup>†</sup>	5	1.55	0.10
			sites <sup>†</sup> × day/night	7	1.85	0.09
day/night			5	1.96	0.08	
Slope > 30°			null	4	0.00	0.27
Slope > 30°		sex	5	1.13	0.15	
		sites <sup>†</sup>	5	1.71	0.11	
		day/night	5	2.01	0.10	
		Moorlands	null	4	0.00	0.29
		sex	5	1.49	0.14	
		day/night	5	1.88	0.11	
Slope < 10°		sites <sup>†</sup>	5	1.99	0.11	
		sites <sup>†</sup>	5	0.00	0.26	
		sex + sites <sup>†</sup>	6	0.94	0.16	
		Activity	sites	9	0.00	0.68
		disturb	7	1.55	0.32	
		<i>(B) Hunting period</i>				
Movement sinuosity	2 h	disturb	5	0.00	0.39	
		sites	6	1.81	0.16	
	20 min	sex × day/night × sites <sup>†</sup>	11	0.00	0.23	
		sites <sup>†</sup> × day/night + sex × day/night	9	0.91	0.15	
		sex × day/night	7	1.41	0.11	
		sex × day/night + sites <sup>†</sup>	8	1.49	0.10	
		sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	1.84	0.09	
		Habitat use	Forest	sites <sup>†</sup>	5	0.00
	Habitat use	Forest	null	4	0.39	0.17
			sites <sup>†</sup> + day/night	6	1.23	0.11
day/night			5	1.61	0.09	
sex + sites <sup>†</sup>			6	1.98	0.08	
Slope > 30°			sex × day/night	7	0.00	0.13
null			4	0.41	0.10	
Slope > 30°		day/night	5	0.92	0.08	
		sex × sites <sup>†</sup> + sex × day/night	9	1.08	0.07	
		sex × sites <sup>†</sup>	7	1.16	0.07	
		sex	5	1.42	0.06	
		sex × day/night + sites <sup>†</sup>	8	1.46	0.06	
		sex + sites <sup>†</sup>	6	1.54	0.06	
		sex × sites <sup>†</sup> + day/night	8	1.69	0.05	
		sites <sup>†</sup>	5	1.77	0.05	
		sex + day/night	6	1.98	0.05	
		Moorlands	sex × day/night	7	0.00	0.36
		sex × day/night + sites <sup>†</sup>	8	1.58	0.16	
		Slope < 10°	sex × day/night	7	0.00	0.29
sex + day/night	6		1.35	0.15		
sex × day/night + sites <sup>†</sup>	8		1.90	0.11		
Activity	disturb		7	0.00	0.73	

The acronyms of the 3 studied areas were derived from the combination of “t” = low tourism pressure, “T” = high tourism pressure, “h” = low hunting pressure, “H” = high hunting pressure (see Table 1A and Appendix A for details). For each behavioral characteristic, differences between data recorded on Sundays and on Mondays were computed for each individual and each 48 h periods of monitoring. The models examined (linear mixed effect models for movements sinuosity and habitat use, generalized additive mixed models for activity patterns) either opposed disturbed areas from undisturbed ones (hereafter called “disturb”; tourism period = TH versus th-tH; hunting period = tH-TH versus th, respectively) or all possible areas (sites = th versus tH versus TH; sites<sup>†</sup> = tH versus TH) and tested for variable responses between sexes and between periods of intense/low human activities (i.e. day/night, except for movement sinuosity at the 2 h scale), and all two- and three-way interactions. Only models with  $\Delta AIC_c < 2$  are presented here and were used to compute model-averaged coefficients represented in Figs. 3–5. For full lists of models fitted, see Appendix B. K = number of parameters;  $\Delta AIC_c$  = difference in Akaike Information Criterion with second-order adjustment;  $AIC_c w$  = Akaike weight.

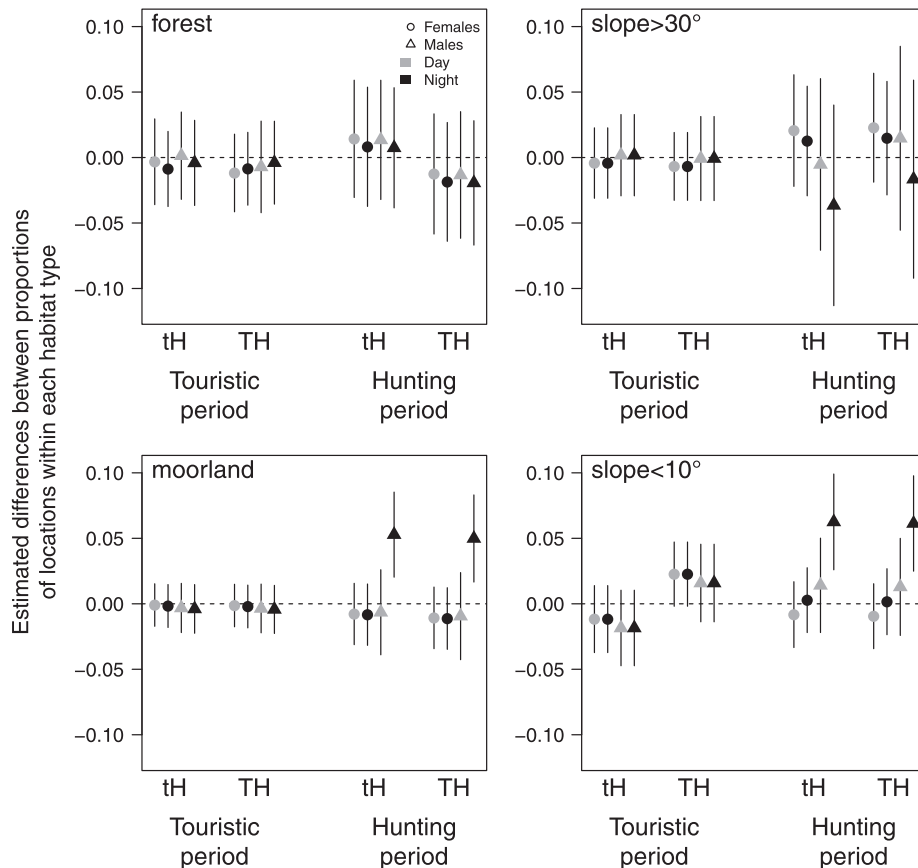
during daytime and were conversely more sinuous during nights following hunting (Table 2 and Fig. 3B). Of note, in terms of step length only, an increase of 18.9% (95% CI: [5.5; 32.3], i.e. +24.9 m · 2 h<sup>-1</sup>; 95% CI: [9.4; 40.5]) occurred during disturbed days compared with undisturbed days during hunting period.

### 3.2. Habitat use

During touristic period, the use of safe (forests and slope >30°), unsafe (slope <10°) and/or favorable areas for foraging (moorlands) did not differ between Sundays and Mondays (95% confidence



**Fig. 3.** Tourism (A) and hunting (B) impacts on the daily sinuosity of movements of GPS-collared Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in the Caroux-Espinouse massif (southern France) between 2003 and 2012. These impacts were analyzed at two temporal scales (2 h and 20 min) in a protected reserve (th, where tourism pressure is low and restricted to main trails, and hunting is forbidden) and two surrounding unprotected areas (tH, where tourism pressure is high, and TH, where tourism pressure is low, and both of them being harvested areas). Daily sinuosity was assessed using a sinuosity index SI (Benhamou, 2004; see text for details). Model-averaged coefficients and 95% confidence intervals (CI) are derived from the set of linear mixed-effect models, including individuals and 48 h periods as grouping factors to account for repeated measures, with  $\Delta AIC_c < 2$  (see Table 2 for details).



**Fig. 4.** Tourism and hunting impacts on use of safe habitats (forests and slope  $> 30^\circ$ ), unsafe habitats (slope  $< 10^\circ$ ) and/or habitats providing the best foraging conditions (moorlands) by GPS-collared Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in two unprotected areas (tH, where tourism pressure is low, and TH, where tourism pressure is high, both of them being harvested areas) of the Caroux-Espinouse massif (southern France). Model-averaged coefficients and 95% confidence intervals (CI) are derived from the set of best linear mixed-effect models, including individuals and 48 h periods as grouping factors to account for repeated measures, with  $\Delta AIC_c < 2$  (see Table 2 for details).

intervals including 0 for each habitat variable; Table 2 and Fig. 4). This was also the case for use of safe habitats (forests and slope  $> 30^\circ$ ) during hunting period in both hunted areas (Table 2 and Fig. 4). However, contrasted temporal patterns were observed between both sexes in their use of slope  $< 10^\circ$  and moorlands during the same period with males increasing their use of these areas during nights following hunting (Table 2 and Fig. 4).

### 3.3. Activity pattern

During touristic period, contrasted daily patterns of differences in hourly activity (pA) were found between animals facing high or low touristic pressure (Table 2). Whereas no significant response was revealed in th and tH areas (no 24 h variation in pA at the daily scale and 95% CI including 0, Fig. 5A), mouflon were generally less

active during the day (08:45–17:30 UTC; on average [95% CI]  $-3.9\%$  [ $-6.0; -1.7$ ]; maximum difference of  $-5.0\%$  [ $-7.1; -2.9$ ]) and more active during the night (21:00–01:00 UTC; on average  $+3.2\%$  [ $1.1; 5.2$ ]; maximum difference of  $+3.7\%$  [ $1.8; 5.7$ ]) on Sundays than on Mondays in TH area (Fig. 5A).

During hunting period, changes in activity patterns between Sundays and Mondays were revealed in the 3 areas, with contrasted responses between individuals from th and individuals from the hunted areas (tH and TH, Table 2 and Fig. 5B). We observed a decrease in diurnal activity (09:00–20:00 UTC;  $-2.1\%$  [ $-3.5; -0.8$ ]; maximum difference of  $-2.6\%$  [ $-4.1; -1.3$ ]) in th during day period only, whereas a much marked decrease in activity rate was found in hunted areas (08:15–16:45 UTC;  $-3.9\%$  [ $-6.0; -1.8$ ]; maximum difference of  $-5.0\%$  [ $-7.0; -3.0$ ]) followed by a subsequent increase during the first half of the night (19:30–23:45 UTC;  $+3.1\%$  [ $1.1; 5.1$ ]; maximum difference of  $+3.8\%$  [ $1.7; 5.9$ ]).

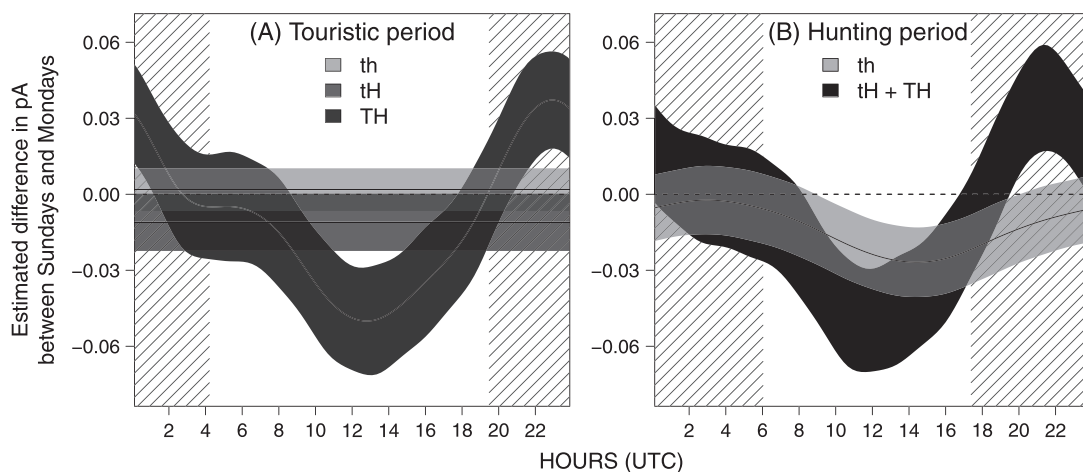
#### 4. Discussion

Our analyses revealed hunting and tourism had different impact on movements, space use and daily activity budget of Mediterranean mouflon. Accordingly, whether we contrasted days or areas with low and high touristic pressure, the only response we found was a pronounced shift in the day/night allocation of activities in the most visited area. Mouflon that were less disturbed in the two other areas did not display any direct or indirect response to the presence of tourists, exemplifying the fine-scale behavioral response to this source of non-lethal disturbance. Alternatively, hunting was disruptive with both immediate responses in terms of less sinuous movements and decreased daytime activities, and a delayed compensatory response in terms of increased movement sinuosity, use of unsafe/foraging areas, and activity level during nighttime. Even animals living in the wildlife reserve, where no hunting occurred, displayed a modified daily activity budget during hunting period, though less pronounced than in the hunted areas. We further detected sex-differences in the response to hunting only.

As predicted from risk-disturbance hypothesis (Frid and Dill, 2002), both males and females from hunted areas shifted foraging activities from daytime (less active, females tended to perform longer and straighter, i.e. non-foraging, movements, Van Moorter

et al., 2010) to nocturnal hours (more active, more sinuous movements by females and increased use of the areas concentrating mouflon food by males; Baudière, 1970; Cransac et al., 1997; Marchand et al., 2013) as a strategy to avoid intense and temporally predictable hunting activities. In this dimorphic/polygynous species, males and females exhibited widely divergent life-history tactics (i.e. sexual segregation) probably explaining sex-specific responses as a result of different levels of exposure or of different compensatory strategies related to habitat segregation (Cransac and Hewison, 1997; Singh et al., 2010). Indeed, our results suggested that the compensatory strategy of males during nights following hunting disturbance consisted in increasing foraging activities on the most profitable habitats (moorlands on plateaux; Marchand et al., 2014), involving longer movements between resting and foraging areas and hence, no difference in movement sinuosity between nights following disturbed or undisturbed days. Females may rather concentrate foraging activities around resting places, and hence performed more sinuous movements during nights following disturbance. Such sex-specific strategies regarding use of unsafe plateaux has already been described during lambing and summer periods in this population (Marchand et al., 2014).

The strategy of mouflon during hunting period, close to predictions from predation risk allocation hypothesis and optimization trade-offs in predator-prey relationships (Lima and Dill, 1990; Lima, 1998; Lima and Bednekoff, 1999; Ferrari et al., 2009) has already been documented in disturbed birds (Burger and Gochfeld, 1991; Bélanger and Bédard, 1995). This strategy is often hypothesized as an explanation to shifts in the activity pattern of mammals coping with intense human activities (Kaczensky et al., 2006; Ohashi et al., 2013; Podgórski et al., 2013). However, these behavioral disruptions raised questions on the energetic costs for mouflon and would require further research on their long-term fitness consequences (Gill and Sutherland, 2000; Beale and Monaghan, 2004; Beale, 2007). Indeed, we may expect that increasing nocturnal foraging, in particular in unsafe areas, could take a heavy toll, e.g. in terms of stress, physiological consequences and resulting energy expenditure (Hayes et al., 1994), on this species generally described as crepuscular (Bourgoin et al., 2011) and for which visibility has been identified as a key factor in anti-predator behaviors (Benoist et al., 2013; in other wild sheep species, see Risenhoover and Bailey, 1985; Hayes et al., 1994). This could be particularly detrimental when carried out during the adverse



**Fig. 5.** Daily patterns of differences in proportions of time active per hour (pA) in GPS-collared Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) living in a protected reserve (th, where tourism pressure is low and restricted to main trails, and hunting is forbidden) and two surrounding unprotected areas (tH, where tourism pressure is low, and TH, where tourism pressure is high, both of them being harvested areas) of the Caroux-Espinouse massif (southern France). Solid lines and gray areas represent model-averaged differences in pA and 95% confidence intervals derived from the set of best GAMMs models, including individuals and 48 h periods as grouping factors to account for repeated measures, with  $\Delta AICc < 2$  (see Table 2 for details). Dashed lines indicated 0, i.e. no differences between Sundays and Mondays. Light gray shaded areas represent the nocturnal period between the mean morning and evening civil twilights (sun  $6^\circ$  below the horizon) of the 48 h periods included in each analysis.



season and the breeding period (Garel et al., 2011). Compensatory mechanisms that have sometimes been reported (e.g. shorter feeding time can be compensated by increasing instantaneous intake rate, Iason et al., 1999), often occur at the expense of other fitness-enhancing activities (e.g. vigilance; Beauchamp, 2007) and disturbance often results in energetic costs (Gill and Sutherland, 2000; Williams et al., 2006; Naylor et al., 2009) and negative impacts on fitness (Phillips and Alldredge, 2000; French et al., 2011).

By contrast, the only response of animals living in the area protected from hunting occurred on activity rate and did not result in a nocturnal compensatory response, suggesting that costs of such responses for protected animals were limited. This behavioral disruption in the contiguous wildlife reserve has also been revealed during hunting period in the vigilance behavior of males of this population (Benoist et al., 2013) and was interpreted as a pervasive effect of hunting. Indeed, mouflon were not strictly restricted to the protected area and punctual movements of individuals to the harvested surroundings of the protected area occurred (in the present study, <9% of locations of GPS-collared mouflon from th were outside the protected area; see also Dubois et al., 1993; Benoist et al., 2013). In addition, the small size (1 704 ha), the shape (a long but narrow area) and the configuration (mostly covering a unique valley) of this area might not totally buffer mouflon from perceptible hunting indirect stimuli (e.g. shooting or barking hounds). This result would underline the importance of geographical characteristics of protected areas that should be defined to meet the biological characteristics of the focal species (Diamond, 1975; Soulé and Simberloff, 1986).

The daily activity pattern of individuals living in the area with the most intense touristic pressure (TH = Caroux) was modified during touristic period. However, tourists did not affect movements sinuosity and habitat use whereas hunters did, revealing a rare case of context-specific response in this group of Mediterranean mouflon facing both lethal and non-lethal human disturbances. These results suggest that animals were able to detect cues allowing them to distinguish between hunters/hunting period and predation-free recreationists/touristic period, to correctly balance costs and benefits of human avoidance and choose an appropriate behavioral response (Ydenberg and Dill, 1986). Such abilities in cues detection were reported in other studies (for example dogs: MacArthur et al., 1982; Martinetto and Cugnasse, 2001; on- or off-trail recreation: Miller et al., 2001) and are often proposed to explain contrasted responses of individuals facing with either numerous recreational activities (Naylor et al., 2009) or numerous hunting techniques (Grignolio et al., 2011; Thurffjell et al., 2013). On the other hand, the absence of undisturbed areas within the site where touristic pressure was the highest largely contrasted with the intense but localized disturbance stimuli imposed by driven hunts with hounds. Indeed, unlike hunters, hikers used an extensive network of trails (Fig. 1) resulting in a diffusive presence of numerous tourist groups for most of the day. Such contrasted conditions could also explain these divergent responses, given that decisions concerning avoidance of an habitat should depend on the existence and availability of undisturbed sites and on the quality of both disturbed and undisturbed areas (Ydenberg and Dill, 1986; Gill et al., 2001). Further research, based on a precise assessment of spatio-temporal distributions and intensity of human activities within each area during both periods (see e.g. Sunde et al., 2009), or an experimental design, could help firmly conclude on this pattern. However, experimental disturbance allow studying direct response only (Miller et al., 2001; Lusseau and Bejder, 2007), while we showed here that the consequences of both human activities on animal behavior differed according to the 3 behavioral responses analyzed and were prolonged during low-risk periods. Accordingly, our study call for more studies taking advantage of

indirect methods (GPS and activity loggers) in pseudo-experimental settings when manipulating drivers of disturbance is tricky (see e.g. Sunde et al., 2009; Tolon et al., 2009).

## 5. Management and conservation implications

We clearly showed that intense human activities were strongly correlated with mouflon spatial and temporal behavior in this population, and that these behavioral responses depended on the nature and the level of exposure of animals to human activities. We disclosed here that a protected area (i.e. th) was an efficient tool to reduce human impacts (shaky concept) and should hence be promoted (Knight and Temple, 1995). Spatial restrictions on tourism allowed buffering animals from human activities during touristic period without totally banning it, an essential result for their acceptance and more generally to promote the role of such areas for people environmental awareness and education. This is also interesting as Mediterranean mouflon is a species with both management and conservation concerns (Shackleton and IUCN/SSC Caprinae Specialist Group, 1997). By contrast, strong and consistent responses were revealed in the two harvested areas during hunting period, highlighting another side-effects of such activity in this population (Garel et al., 2007; Benoist et al., 2013). Management policies preventing animals from additional human costs during this period coinciding with adverse season and breeding period in this population should hence be promoted. For instance, stalking occurred during hunting period on Mondays in our area but was shown to involve less disturbance than driven hunt with hounds in our analyses. It should hence be favored, so that temporal restrictions on hunting during breeding periods (Apollonio et al., 2011). Increasing evidence of behavioral disruptions in harvested populations should particularly alert managers regarding recent findings on evolutionary consequences of hunting (Coltman et al., 2003 in bighorn sheep *Ovis canadensis*, Gamelon et al., 2011 in wild boar *Sus scrofa scrofa*, Ciuti et al., 2012 in elk *Cervus elaphus*) to better grasp the whole consequences of increasing human influence in natural areas.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.05.022>.

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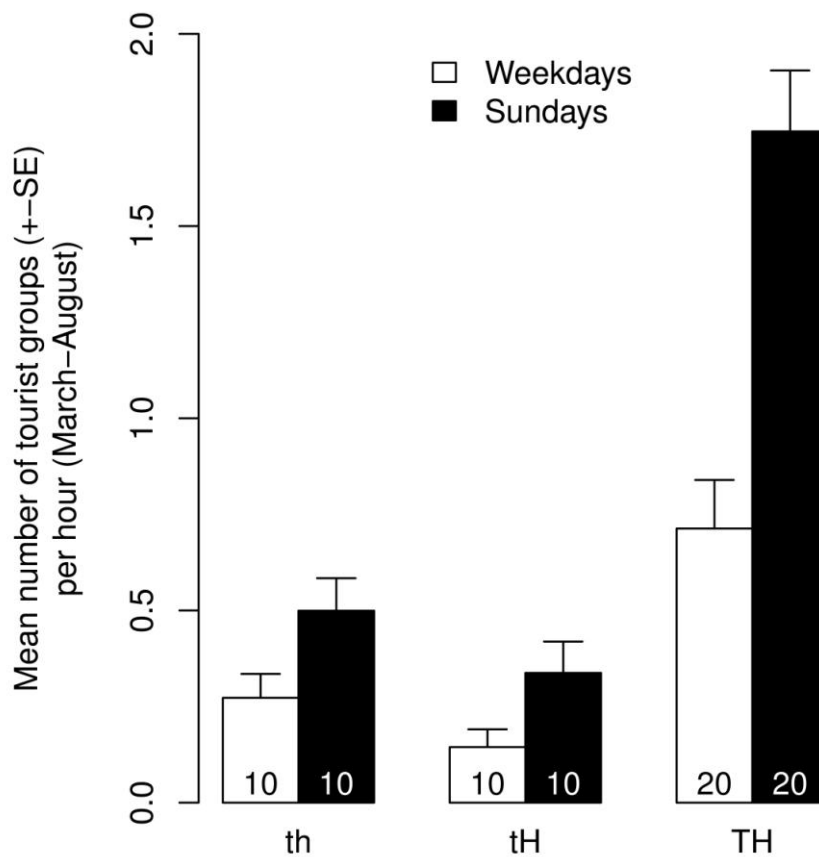
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1 **Appendix A. Assessment of tourism pressure during March-August period**

2 From March to August 1996, tourism pressure in the Caroux-Espinouse massif (southern  
3 France) was assessed by counting the number of groups hiking on the main trails (see Figure  
4 1) in the 3 studied areas (th, tH and TH) on both Sundays and weekdays (see Martinetto et al.  
5 1998 for details). The acronyms of the 3 studied areas were derived from the combination of  
6 "t" = low tourism pressure, "T" = high tourism pressure, "h" = low hunting pressure, "H" =  
7 high hunting pressure (see Table 2A for details). The numbers of repetitions in each area are  
8 reported above x-axis. Although data were recorded in 1996, tourism pressure during our  
9 study period (2003-2012) was not expected to deviate from these trends regarding both  
10 differences between areas and differences between Sundays and weekdays.



1 **Appendix B. Full list of models fitted to investigate (A) tourism and (B) hunting**  
2 **disturbance on movements sinuosity (scales = 2 h and 20 min), habitat use and activity**  
3 **patterns of 66 GPS-collared Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.)**  
4 **living in the Caroux-Espinouse massif (southern France), between 2003 and 2012.**

5 The acronyms of the 3 studied areas were derived from the combination of "t" = low tourism  
6 pressure, "T" = high tourism pressure, "h" = low hunting pressure, "H" = high hunting  
7 pressure (see Table 1A and Appendix A for details). For each behavioral characteristics,  
8 differences between data recorded on Sundays and on Mondays were computed for each  
9 individual and each 48 h periods of monitoring. The models examined (linear mixed effect  
10 models for movements sinuosity and habitat use, generalized additive mixed models for  
11 activity patterns) either opposed disturbed areas from undisturbed ones (hereafter called  
12 "disturb"; tourism period = TH versus th-tH, respectively; hunting period = tH-TH versus th,  
13 respectively) or all possible areas (sites = th versus tH versus TH; sites<sup>†</sup> = tH versus TH) and  
14 tested for variable responses between sexes and between periods of intense/low human  
15 activities (i.e. day/night, except for movement sinuosity at the 2 h scale), and all two- and  
16 three-way interactions. Model-averaged coefficients derived from the set of models with  
17  $\Delta AIC_c < 2$  are represented on Figures 3, 4 and 5. K=number of parameters;  $\Delta AIC_c =$   
18 difference in Akaike Information Criterion with second-order adjustment. ;  $AIC_c w =$  Akaike  
19 weight.

(A) Tourism period

		Models	K	$\Delta AIC_c$	$AIC_c w$
Movement sinuosity	2 h	null	4	0	0.40
		sex	5	1.40	0.20
		disturb	5	1.79	0.17
		sex + disturb	6	3.22	0.08
		sites	6	3.67	0.07
		sex × disturb	7	4.92	0.03
		sex + sites	7	5.13	0.03
		sex × sites	9	6.84	0.01
	20 min	null	4	0.00	0.29



	day/night	5	1.85	0.12
	sex	5	1.95	0.11
	sites <sup>†</sup>	5	2.02	0.11
	sex × day/night	7	2.55	0.08
	sex + sites <sup>†</sup>	6	3.97	0.04
	sex + day/night	6	3.81	0.04
	sites <sup>†</sup> + day/night	6	3.87	0.04
	sex × day/night + sites <sup>†</sup>	8	4.58	0.03
	sites <sup>†</sup> × day/night	7	4.98	0.02
	sites <sup>†</sup> × day/night + sex × day/night	9	5.47	0.02
	sex × sites <sup>†</sup>	7	5.68	0.02
	sex + sites <sup>†</sup> + day/night	7	5.84	0.02
	sex × sites <sup>†</sup> + sex × day/night	9	6.30	0.01
	sites <sup>†</sup> × day/night + sex	8	6.95	0.01
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	7.20	0.01
	sex × sites <sup>†</sup> + day/night	8	7.55	0.01
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	8.67	0.00
	sex × day/night × sites <sup>†</sup>	11	8.88	0.00
	null	4	0	0.22
	sex	5	0.96	0.14
	sites <sup>†</sup>	5	1.55	0.10
	sites <sup>†</sup> × day/night	7	1.85	0.09
	day/night	5	1.96	0.08
	sex + sites <sup>†</sup>	6	2.59	0.06
	sites <sup>†</sup> × day/night + sex	8	2.90	0.05
	sex + day/night	6	2.92	0.05
	sites <sup>†</sup> + day/night	6	3.51	0.04
forest	sex × sites <sup>†</sup>	7	3.46	0.04
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	3.78	0.03
	sex + sites <sup>†</sup> + day/night	7	4.56	0.02
	sites <sup>†</sup> × day/night + sex × day/night	9	4.90	0.02
	sex × day/night	7	4.95	0.02
	sex × sites <sup>†</sup> + day/night	8	5.43	0.01
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	5.78	0.01
	sex × day/night + sites <sup>†</sup>	8	6.59	0.01
Habitat use	sex × sites <sup>†</sup> + sex × day/night	9	7.47	0.01
	sex × day/night × sites <sup>†</sup>	11	7.74	0.00
	null	4	0.00	0.27
	sex	5	1.13	0.15
	sites <sup>†</sup>	5	1.71	0.11
	day/night	5	2.01	0.10
	sex + sites <sup>†</sup>	6	2.92	0.06
	sex + day/night	6	3.15	0.06
	sex × sites <sup>†</sup>	7	3.43	0.05
slope >30°	sites <sup>†</sup> + day/night	6	3.73	0.04
	sex × day/night	7	4.04	0.04
	sex + sites <sup>†</sup> + day/night	7	4.94	0.02
	sites <sup>†</sup> × day/night	7	5.21	0.02
	sex × sites <sup>†</sup> + day/night	8	5.46	0.02
	sites <sup>†</sup> × day/night + sex	8	5.78	0.01
	sex × day/night + sites <sup>†</sup>	8	5.84	0.01
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	6.30	0.01
	sex × sites <sup>†</sup> + sex × day/night	9	6.36	0.01

		sites <sup>†</sup> × day/night + sex × day/night	9	6.85	0.01
		sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	7.37	0.01
		sex × day/night × sites <sup>†</sup>	11	9.11	0.00
		null	4	0.00	0.29
		sex	5	1.49	0.14
		day/night	5	1.88	0.11
		sites <sup>†</sup>	5	1.99	0.11
		sex + day/night	6	3.37	0.05
		sex + sites <sup>†</sup>	6	3.46	0.05
		sex × day/night	7	3.57	0.05
		sites <sup>†</sup> + day/night	6	3.88	0.04
		sex × sites <sup>†</sup>	7	4.38	0.03
	moorlands	sex + sites <sup>†</sup> + day/night	7	5.35	0.02
		sites <sup>†</sup> × day/night	7	5.39	0.02
		sex × day/night + sites <sup>†</sup>	8	5.55	0.02
		sex × sites <sup>†</sup> + day/night	8	6.27	0.01
		sex × sites <sup>†</sup> + sex × day/night	9	6.48	0.01
		sites <sup>†</sup> × day/night + sex	8	6.87	0.01
		sites <sup>†</sup> × day/night + sex × day/night	9	6.91	0.01
		sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	7.80	0.01
		sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	7.84	0.01
		sex × day/night × sites <sup>†</sup>	11	8.05	0.01
		sites <sup>†</sup>	5	0.00	0.26
		sex + sites <sup>†</sup>	6	0.94	0.16
		sites <sup>†</sup> + day/night	6	2.02	0.09
		sex × sites <sup>†</sup>	7	2.17	0.09
		null	4	2.36	0.08
		sex + sites <sup>†</sup> + day/night	7	2.97	0.06
		sex	5	3.02	0.06
		sites <sup>†</sup> × day/night	7	4.05	0.03
		sex × sites <sup>†</sup> + day/night	8	4.20	0.03
	slope < 10°	day/night	5	4.37	0.03
		sex × day/night + sites <sup>†</sup>	8	4.67	0.02
		sites <sup>†</sup> × day/night + sex	8	5.00	0.02
		sex + day/night	6	5.04	0.02
		sex × sites <sup>†</sup> + sex × day/night	9	5.91	0.01
		sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	6.24	0.01
		sites <sup>†</sup> × day/night + sex × day/night	9	6.70	0.01
		sex × day/night	7	6.74	0.01
		sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	7.95	0.01
		sex × day/night × sites <sup>†</sup>	11	9.83	0.00
		sites	9	0.00	0.68
		disturb	7	1.55	0.32
	Activity	sex × disturb	10	12.06	0.00
		sex × sites	13	12.53	0.00
		null	5	19.00	0.00
		sex	7	25.41	0.00

20

## (B) Hunting period

		Models	K	ΔAIC <sub>c</sub>	AIC <sub>c w</sub>
Movement sinuosity	2 h	disturb	5	0.00	0.39
		sites	6	1.81	0.16

	sex + disturb	6	2.01	0.14
	null	4	2.22	0.13
	sex + sites	7	3.83	0.06
	sex × disturb	7	4.04	0.05
	sex	5	4.21	0.05
	sex × sites	9	7.05	0.01
	sex × day/night × sites <sup>†</sup>	11	0.00	0.23
	sites <sup>†</sup> × day/night + sex × day/night	9	0.91	0.15
	sex × day/night	7	1.41	0.11
	sex × day/night + sites <sup>†</sup>	8	1.49	0.10
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	1.84	0.09
	sex × sites <sup>†</sup> + sex × day/night	9	2.42	0.07
	sites <sup>†</sup> × day/night	7	2.90	0.05
	day/night	5	3.19	0.05
	sites <sup>†</sup> + day/night	6	3.19	0.05
20 min	sites <sup>†</sup> × day/night + sex	8	4.52	0.02
	sex + day/night	6	4.73	0.02
	sex + sites <sup>†</sup> + day/night	7	4.80	0.02
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	5.45	0.02
	sex × sites <sup>†</sup> + day/night	8	5.73	0.01
	sites <sup>†</sup>	5	22.73	0.00
	null	4	22.76	0.00
	sex	5	24.30	0.00
	sex + sites <sup>†</sup>	6	24.30	0.00
	sex × sites <sup>†</sup>	7	25.28	0.00
	sites <sup>†</sup>	5	0.00	0.20
	null	4	0.39	0.17
	sites <sup>†</sup> + day/night	6	1.23	0.11
	day/night	5	1.61	0.09
	sex + sites <sup>†</sup>	6	1.98	0.08
	sites <sup>†</sup> × day/night	7	2.25	0.07
	sex	5	2.40	0.06
	sex + sites <sup>†</sup> + day/night	7	3.21	0.04
	sex + day/night	6	3.63	0.03
forest	sex × sites <sup>†</sup>	7	3.88	0.03
	sites <sup>†</sup> × day/night + sex	8	4.24	0.02
	sex × day/night + sites <sup>†</sup>	8	4.59	0.02
	sex × day/night	7	4.99	0.02
	sex × sites <sup>†</sup> + day/night	8	5.12	0.02
	sites <sup>†</sup> × day/night + sex × day/night	9	5.51	0.01
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	6.14	0.01
	sex × sites <sup>†</sup> + sex × day/night	9	6.49	0.01
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	7.43	0.00
	sex × day/night × sites <sup>†</sup>	11	9.50	0.00
	sex × day/night	7	0.00	0.13
	null	4	0.41	0.10
	day/night	5	0.92	0.08
	sex × sites <sup>†</sup> + sex × day/night	9	1.08	0.07
slope >30°	sex × sites <sup>†</sup>	7	1.16	0.07
	sex	5	1.42	0.06
	sex × day/night + sites <sup>†</sup>	8	1.46	0.06
	sex + sites <sup>†</sup>	6	1.54	0.06
	sex × sites <sup>†</sup> + day/night	8	1.69	0.05

	sites <sup>†</sup>	5	1.77	0.05
	sex + day/night	6	1.98	0.05
	sex + sites <sup>†</sup> + day/night	7	2.07	0.05
	sites <sup>†</sup> + day/night	6	2.28	0.04
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	2.95	0.03
	sites <sup>†</sup> × day/night + sex × day/night	9	3.32	0.02
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	3.62	0.02
	sites <sup>†</sup> × day/night + sex	8	4.00	0.02
	sites <sup>†</sup> × day/night	7	4.21	0.02
	sex × day/night × sites <sup>†</sup>	11	4.97	0.01
	null	4	6.15	0.02
	sex	5	3.46	0.06
	sites <sup>†</sup>	5	7.53	0.00
	day/night	5	5.91	0.02
	sex + sites <sup>†</sup>	6	5.03	0.03
	sex + day/night	6	3.23	0.07
	sites <sup>†</sup> + day/night	6	7.30	0.01
	sex × sites <sup>†</sup>	7	6.57	0.01
	sex + sites <sup>†</sup> + day/night	7	4.81	0.03
moorlands	sex × day/night	7	0.00	0.36
	sites <sup>†</sup> × day/night	7	9.02	0.00
	sex × sites <sup>†</sup> + day/night	8	6.35	0.01
	sex × day/night + sites <sup>†</sup>	8	1.58	0.16
	sites <sup>†</sup> × day/night + sex	8	6.53	0.01
	sex × sites <sup>†</sup> + sex × day/night	9	3.14	0.07
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	3.44	0.06
	sites <sup>†</sup> × day/night + sex × day/night	9	8.08	0.01
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	5.00	0.03
	sex × day/night × sites <sup>†</sup>	11	6.71	0.01
	sex × day/night	7	0.00	0.29
	sex + day/night	6	1.35	0.15
	sex × day/night + sites <sup>†</sup>	8	1.90	0.11
	sex	5	2.43	0.09
	sex × sites <sup>†</sup> + sex × day/night	9	3.23	0.06
	sex + sites <sup>†</sup> + day/night	7	3.24	0.06
	sites <sup>†</sup> × day/night + sex × day/night	9	3.95	0.04
	sex × day/night × sites <sup>†</sup>	11	4.25	0.04
	sex + sites <sup>†</sup>	6	4.32	0.03
	sex × sites <sup>†</sup> + day/night	8	4.57	0.03
	sex × sites <sup>†</sup> + sex × day/night + sites <sup>†</sup> × day/night	10	5.28	0.02
	sites <sup>†</sup> × day/night + sex	8	5.29	0.02
	sex × sites <sup>†</sup>	7	5.64	0.02
	day/night	5	6.53	0.01
	sites <sup>†</sup> × day/night + sex × sites <sup>†</sup>	9	6.62	0.01
	null	4	7.58	0.01
	sites <sup>†</sup> + day/night	6	8.23	0.00
	sites <sup>†</sup>	5	9.27	0.00
	sites <sup>†</sup> × day/night	7	10.27	0.00
	disturb	7	0.00	0.73
Activity	null	5	2.71	0.19
	sex	7	4.83	0.07
	sex × disturb	10	7.73	0.01
	sites	9	9.18	0.00

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21	sex × sites	13	19.98	0.00
22				

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