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Human disturbance, habitat characteristics and social environment generate sex-specific responses in vigilance of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.)

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Human disturbance, habitat characteristics and social environment generate sex-specific responses in vigilance of Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp.)

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ABSTRACT

Vigilance is an important part of decision making process in ungulates related to risk effects. Thus, understanding the mechanisms shaping vigilance behavior provides an insight on factors influencing fitness variation between individuals. We compared several factors (human disturbance, habitat, social and individual characteristics) influencing males' and females' vigilance behavior in a population of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp) inhabiting the massif of Caroux-Espinouse (France) using a scan sampling protocol. For both males and females, yearlings were less vigilant than adults, as they faced a crucial period of high food requirements and lacked foraging experience. Both sexes were less vigilant in the protected area (with no hunting and restricted tourism) compared to disturbed areas (with hunting and tourism). Nonetheless, during the hunting period, males were as vigilant in and out of the protected area. This is explained by the fact that the rutting period is the same as the hunting season, and the rut increases males' vigilance in a context of social dominance. Females with lamb were more vigilant than non-reproductive females. Females without lamb were not vigilant at all in groups with lambs, but in groups with no lambs, these females were highly vigilant. Finally, habitat characteristics, such as visibility for females (vigilance decreased in a habitat with a good visibility) and quality of feeding sites for males (vigilance decreased in high quality feeding sites), also contributed to explain variations in the level of vigilance. Thus our multifactorial study allows to support the importance of favorable habitat (open areas and high food quality) and the existence of protected areas for the management and conservation of wild sheep.

Keywords: habitat characteristics, hunting, individual characteristics, Mediterranean mouflon, protected area, risk effects, social characteristics, tourism, vigilance.

Contents

INTRODUCTION 1

MATERIALS AND METHODS 4

- Study area and population 4
- Data collection 5
- Spatial covariates 6
- Data analysis and model selection 7

RESULTS 9

- Data and model selection 9
- Human disturbances and habitat characteristics 10
- Quality of feeding sites 10
- Intrinsic factors and social environment 11

DISCUSSION 11

ACKNOWLEDGMENTS 15

REFERENCES 16

APPENDIX A: Model selection with AICc 31

REMERCIEMENTS 33

INTRODUCTION

Predators may impact large herbivores demography both through lethal direct effects, and lethal and non-lethal indirect effects (Lima and Dill, 1990; Ludwig and Rowe, 1990; Lima, 1998). Indirect effects depend on how predators cause adaptive shifts in prey behavior or life history allocation (Schmitz et al. 1997, Creel and Christianson 2008). Indirect lethal effects arise through the increase of starvation risk when prey reduce foraging time to reduce predation hazard (Hik, 1995). Non-lethal indirect effects are expected when prey alter their life history strategies and habitat selection in response to predation risk (Dodson and Havel, 1988; Skelly and Werner, 1990; Werner, 1991). These behavioral changes due to predators are known as risk effects (Schmitz et al. 1997, Boonstra et al. 1998, Creel and Christianson 2008). Previous studies have shown that risk effects can impact prey dynamics even more than the direct mortality due to killing by predators (Brown et al., 1999, Creel and Christianson 2008). As an example, vigilance behavior arises at the expense of feeding under certain circumstances (Blanchard and Fritz, 2007), and thus may impact fitness over the long term (Watson et al., 2007).

Because an important role of vigilance behavior is the detection and avoidance of predators (Dimond and Lazarus, 1974), the time an animal spends scanning its surroundings can be used as a proxy of the perception of risk. Hence a better understanding of the factors shaping vigilance behavior should help to provide insight into spatial, temporal and inter-individual variation in risk effects, as well as mechanisms causing fitness variation between individuals (Van Noordwijk and Dejong, 1986).

Human disturbance shapes the structures and functions of ecosystems. Anthropic pressures such as tourism or hunting practices have often been shown to increase the level of vigilance, because they are commonly perceived as a risk by wild animals (Douglas, 1971; Cerderna and Lovari, 1985). Beyond human disturbances, characteristics of environment related to the risk of predation, such as habitat visibility, are also well-known to influence the vigilance behavior (in African antelopes Underwood, 1982; Desportes and al., 1987). For instance a low visibility has been shown to increase springboks' vigilance, *Antidorcas marsupialis* (Bednekoff and Ritter, 1994).

Many other factors also influence vigilance behavior. Among them, increasing group size has been repeatedly reported to decrease individual vigilance (Pulliam, 1973; Elgar, 1989) because of a dilution effect (Hamilton, 1971; Foster and Treherne, 1981; Dehn, 1990), a many-eyes effect (Pulliam, 1973; Lazarus, 1979) or as a result of an increase in intragroup competition (Beauchamp, 2003). Further, intrinsic factors such as age and reproductive status are expected to interact with social environment, such as group composition, to shape vigilance patterns. Older individuals would be more vigilant than younger conspecifics because of the difference in growth tactics (Metcalfe and Furness, 1984). In large herbivores most of the growth takes place during the first years of life (e.g. Garel et al., 2009 in chamois *Rupicapra rupicapra*) during which young animals can be expected to trade vigilance in order to undertake high food requirement. This risky behavior could be balanced by relying on adult experience present in the groups which have acquired skills in allocating their time efficiently between potentially conflicting activities such as foraging, avoiding predators and interacting with conspecifics (reviewed in Sullivan, 1988). As in other dimorphic ungulates, males and females differ in their life history tactics, with males relying on their body condition and females on offspring survival (Ralls, 1977; Ruckstuhl and Nehaus, 2002; Mooring, 2003). Thus females with young are expected to be the most vigilant class (Bergerud, 1974; Hunter and Skinner, 1998; Laundré et al., 2001; Childress and Lung, 2003; Hamel and Côté, 2007), non-reproductive females and males probably benefit from the higher investment in vigilance by reproducing females to reduce their own vigilance when foraging in the same group (Carter et al., 2009). At the annual scale, reproductive period should result into an increase in the level of vigilance in females (during births) because of the vulnerability of their young (Childress and Lung, 2003), but also in males (during rut) in a context of social dominance (Bon et al., 1992).

Here, we aimed at studying the factors influencing male and female vigilance behavior in a population of Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp.) facing with low natural predation and marked human pressures (hunting and recreational activities; Martinetto et al., 1998). We took advantage of spatial ([HA] with hunting and tourism area vs Wildlife Reserve [WR] without hunting and with restricted recreational activities) and temporal (hunting vs non-hunting period) variation in term of human pressure to assess the relative roles of extrinsic (disturbance, visibility, group size and composition) and intrinsic (age, reproductive status) factors in shaping vigilance patterns (Table 1). In our population, some females have horns while others do not. Because the defense faculties provided by horns of females (Berger, 1978) may lead to a decrease in their time spent in vigilance as compared to hornless females, we included the horn phenotype of females in our analysis. We expected a lower level of vigilance of mouflon located in the WR compared to animals located in the HA, and that the magnitude of such an effect increases during the hunting period (Grignolio et al., 2011). As factors shaping vigilance behavior, such as habitat characteristics, may also depend on food quality (Fortin et al., 2004; Blanchard and Fritz 2007; Benhaiem, 2008), we also included patch quality in our analysis (Table 1).

Few studies have assessed concurrently the effects of all of these factors over contrasted time periods (yearly variation) and spatial characteristics (non-protected vs. protected areas), and to our knowledge none have performed such a global approach on the vigilance in Mediterranean mouflon (Table 1).

MATERIALS AND METHODS

Study area and population

The population of mouflon inhabits the Caroux–Espinouse massif (43°38′N, 2°58′E; elevation 150–1124 m a.s.l.) in the Southern border of the Massif Central, in Southern France (Fig.1(A)). The massif consists of high plateaus alternating with deep valleys (Fig.1(B)). Vegetation consists in an irregular mosaic of beech, chestnut, coniferous, ever-green oak with open area dominated by moorlands of heather and broom heathlands. Except in the Wildlife Reserve (WR; Fig.1(B)), hunting occurred from September, 1st to the end of February for mouflon, wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*). Hunters harvested the same number of females and males in order to control population size. Stalking (usually for trophy hunting of the largest horned males; Garel et al. 2007) and driven hunting were the two most common hunting practices. Driven hunting was primarily performed for wild boar hunting during which male and female mouflon were also harvested. Stalking involved the presence of a group of 2±2 humans whereas wild boar hunting involved the presence of numerous hunters and domestic dogs (Maublanc et al., 1992). Human activities were strongly restricted in WR (no hunting, hiking only on one trail across the WR and two bordering it) and accordingly, human disturbance has been found to be much lower than in other parts of the massif (Martinetto et al. 1998).

Roe deer and wild board were the two other free-ranging ungulates inhabiting this massif (at low density comparatively to the mouflon population). Mouflon had not 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 (Cabannel and Cugnasse, 1999).

Most births occurred in April, but the lambing season ranged from late March to June (Bon et al. 1993). The gestation time is of 5 months in mouflon, implying that ewes are fertilized between late October and January (Garel et al. 2005a), but mouflon rams roam from one female group to another and exhibit courtship behavior from the beginning of October (Bon et al., 1992). Accordingly, the whole rutting period may be considered to stretch from October to January. We used this reproductive time period in males and females to define period of social interactions (Table 1).

Mouflon is classified as grazer (*sensu* Hofmann, 1989) including herbaceous species in a large proportion of its diet (40-50% of grasses in our population; Cransac et al., 1997). Accordingly, mouflon fed primarily on open habitats composed of meadows and broom moorlands that offer the highest abundance of herbaceous species (Cazau et al., 2011). We restricted our analysis to these feeding patches and we investigated the role of habitat quality of vigilance behavior (Pays et al., 2011). Specifically, we opposed moorlands (feeding sites of low quality) and meadows/game cultures (feeding sites of high quality) because moorlands are dominated by ligneous species of low digestibility for mouflon (Cransac et al., 1997, Cazau et al., 2011).

Data collection

Data were simultaneously collected along 5 fixed transects (around 13km for each; Fig. 1(B)), walked simultaneously on the entire diurnal period of the day, from March 3rd, 1996 to November 3rd, 1996 (Martinetto et al., 1998). These 5 transects correspond to 5 sectors which cover 29.5% of the population's range (Martinetto et al., 1998). Data were sampled distinctly during weekends (n = 16) and other weekdays (n = 13) to provide contrasted conditions of human disturbance (Martinetto et al. 1998). These transects were chosen to sample the environmental diversity in term of habitat types and human pressures (tourism and hunting) throughout the study area (Martinetto et al., 1998). Spatial coordinates (based on a 125*125m grid size), habitat, group size and group composition in age-sex classes were noted for each group encountered. Although five age-sex classes (including lambs) were identified on the field using principally horn development (males) and size of the white facial mask (females), such criteria are poor indicators of age (Garel et al. 2005b, 2006). Therefore, we chose to distinguish only three age categories: lambs, young (1 year old) and adults (> 1year old). For each mouflon composing the group, we also recorded individual activity (see below), reproductive status (with or without lamb; lamb being observed suckling and/or following its mother) and presence of horns for females (~25.6% of females were horned in this population).

Seven activity items were identified using scan sampling (Altmann, 1974): feeding, resting, in movement, playing, in rut, in flight and vigilant. The vigilance item corresponds to mouflon with their head raised above shoulder level and scanning their surroundings. It has to be noted that a same animal can be repeatedly seen over several days and in the same day because mouflon were not individually marked. Along with the mouflon observation, the number of tourists and groups of tourists, and tourist group size were recorded at each survey, and for each transect (see Martinetto et al. 1998 for more details). Values obtained for a given transect, season and the distinction between weekdays and week-ends were averaged (between 3 and 6 repetitions) to get a proxy of human disturbance experienced by mouflon at such a scale.

Spatial covariates

We computed buffers of 294 ha (males) and 178 ha (females) around group coordinates to obtain average estimates of landscape visibility experienced by each mouflon in a group. Buffer size was computed as the average home range of 46 mouflon (Marchand et al. unpublished data based on 16 males and 30 females**)** trapped and fitted with Lotek GPS collars 3300S (revision 2; Lotek Engineering Inc., Carp, Ontario, Canada). Visibility layer over the study area was computed using line-of-sight raster analysis function in GRASS which computed, for each pixel, from a height of 1m, the number of visible pixels within a buffer of 600m (that we assumed to be the maximal distance of detection of a predator by mouflon in a fragmented environment). Visibility layer also accounted for the vegetation cover of each pixel (coded open/closed; i.e. from a closed pixel, the number of visible pixels was set to 0).

Data analysis and model selection

We performed sex-specific analysis and tested our hypothesis (see Table 1 for details) using a logistic regression (generalized linear model with binomial distribution and logit link) with vigilance status as the binary dependent variable. We tested for two-way interaction between individual/group characteristics and group size, and between hunting period and protected/unprotected areas. During model selection, we concurrently assessed the effect of variables including characteristics of the animal in the group ("Repro comp. F" and "Age comp."; Table 1) against the related variables centered on the animal only ("Repro" and "Age"). We proceeded similarly with the two variables indexing human pressure (Tourism 1 and 2). Because we only included factors for which we had ≥30 data for each modality, we only used age as a two-factor for females (yearling vs adults). Because we cannot control for pseudo-replication in our data (observation of non-marked animals), we acknowledge parameters estimates can be biased as it is often the case in biological studies (Hurlbert, 2009).

We used backward stepwise selection procedures. We tested successively the main effects of factors and the two way interaction against the most general model by using likelihood-ratio chi-square (Venables and Ripley, 2002). A variable was considered significant when $p< 0.05$. To ensure that we selected the most explanatory variables (Stephens et al., 2005), we also performed the model selection using the Akaike Information Criterion (AIC) with second order adjustment (AICc) to correct for small-sample bias (Burnham and Anderson, 2002; Appendix A). Models with ΔAICc<2 can be considered to be equally supported by the data (Burnham and Anderson, 2002). We used also Akaike weights (AICcw) to compare the relative performance of models in addition to the absolute AICc values. Weights can be interpreted as the probability that a model is the best model, given the data and the set of candidate models. It is also possible to determine the relative importance of each variable by summing the AICcw across all the models in the set where each variable occurs (Burnham and Anderson, 2002).

For all statistical analyses, we used R version 2.13.0 (R Development Core Team, 2011).

RESULTS

Data and model selection

A total of 602 groups were observed on feeding zones over 28 days of observations (13 during the week and 16 during the weekend), among which 558 were females and 654 were males.

We identified two different models for males and females. The best model for males included the interaction between hunting period and the protection status of the area, and additive effects of age and quality of feeding site (Table 2). Including the age composition of the group instead of the age of the individual only (Table 1) did not provide a better fit (χ^2 = 2.068, d.f. = 1, p=0.150), we therefore used the most simple model ("Age" with two modalities). The best model for females included additive effects of age, habitat visibility, protection status of the area and reproductive composition of the group (Table 3). The reproductive status of the group explained the probability of being vigilant for females, more than the individual reproductive status (χ^2 = 6.491, d.f.= 1, p = 0.011) (Table 1). Both for males and females, since the residual deviances were in line with their degrees of freedom, there was no serious reason to question the fit of the best models selected (Venables and Ripley, 2002).

Both in males and females, models selected using backward stepwise selection corresponded to the simplest model included in the best selected models according to AICc (Appendix A) meaning that our approach was rather conservative (principle of parsimony) and avoided inclusion of spurious effects.

In the following results, we reported predicted effect sizes (mean ± standard error [SE]) for the factor levels "low quality" (variable feeding site), "hunting areas" (variable area status), "non-hunting period" (variable hunting period) for both males and females, and for the factor level “female with lamb” (reproductive composition of the group) and for the average visibility (variable visibility) in females.

Human disturbances and habitat characteristics

Males and females were much less often vigilant in WR than in HA (adult females: WR: 0.09% ± 0.8%, n = 25, HA: 9.7% ± 3.5%, n = 79), but only during the non-hunting period for males (Tables 2 and 3, Fig. 2).

However human presence indexed either by the number of humans observed or the number of groups of humans observed was not selected among the best variables in females (Table 3; Appendix A). For males model selection based on AICc suggested, in addition to the selected variables (Table 2), a trend for a decreasing vigilance when the number of group of tourists increased (slope = -0.298, SE= 0.194, p = 0.125; Appendix A). We observed the same trend with the number of tourists (slope = -0.055, SE=0.050, p= 0.268). Moreover, with the model selection with AICc, we found that rutting activity was in some of the best models and during the rut, males seemed to be more vigilant (24.8% ± 9.8%) than outside the rutting period (14.6% ± 2.1%). But the rut factor was not significant ($\chi^2 = 1.793$, d.f.= 1, p = 0.181).

Females were less vigilant when habitat visibility increased (slope= -0.015, SE=0.007; Table 3) whereas no such effect was reported in males (Table 2). For most extreme values (Table 1), vigilance probability of females decreased from 20.3% ± 5.6% to 5.6% ± 2.6%.

Presence of horns did not influence the level of vigilance in females (Table 3).

Quality of feeding sites

Only males were influenced by the quality of feeding sites (Tables 2 and 3). Males were less vigilant when feeding on high quality pastures (2.5% ± 2.4%, n = 34) than on poor quality broom and heather moorlands (14.7% ± 2.1%, n = 285).

Intrinsic factors and social environment

For both sexes there was no effect of group size and reproductive periods (Tables 2 and 3). Age had a significant effect both on the vigilance of males and females, with young (in males: 6.5% ± 2.4%, n = 79, in females: 0.0% ± 0.0%, n = 54) being less vigilant than adults (in males: 14.7% ± 2.1%, n = 285; in females: 12.6% ± 2.3%, n = 215) (Tables 2 and 3). Although not providing a better fit than age alone (see "model selection" section above), age composition of the group suggested than young males with adults (4.1% ± 2.3%, n = 52) had a lower vigilance than groups of yearlings only (11.8% ± 5.5%, n = 27) and groups of adults only (14.7% ± 2.1%, n = 285).

Females without lamb in non-reproductive group and females with a lamb had a similar level of vigilance (9.7% ± 3.5%, n = 79; 12.6% ± 2.3%, n = 215, respectively), whereas non-reproductive females in a group with reproductive females were never observed vigilant (for adults: 0.0% ± 0.0%, n = 42; Table 3). As compared to females, presence of reproductive females in the group did not influence male vigilance (Table 2).

It has to be noted that the model selection performed using AICc ended up with an effect of group size for females (Appendix A). Vigilance would tend to decrease as group size increases (slope = -0.052, SE = 0.039, p = 0.175).

DISCUSSION

We stressed the importance of human disturbance in shaping vigilance patterns with the Wildlife Reserve acting as a refuge. We confirmed that the factors shaping vigilance behavior depended on sex (Loehr et al., 2005). Our data also showed that habitat characteristics affect vigilance behavior in a sex dependent way, with males increasing vigilance when feeding on low quality sites and females decreasing vigilance in open areas. Finally as expected young animals traded vigilance for other activities and non-reproductive females benefited from increasing vigilance of reproductive females.

The WR acted as a refuge protecting animals against human disturbance, called ‘reserve effect’. No-take reserves are sometimes implemented for sustainable population harvesting because they offer opportunities for animals to spatially avoid harvesters, whereas harvesters can benefit in return from the reserve spillover (Tolon et al., 2012). In the WR, risk perception is low, because there is no hunting and tourism is limited. Accordingly, investment in vigilance behaviour decreases as compared to HA. Moreover, the WR is more used during autumn by males with home ranges close to the WR (Maublanc et al., 1992). Such a result was in line with other studies contrasting protected and unprotected areas (Grignolio et al., 2011; Laidlaw, 2000; in wild boars in our study area Cugnasse et al., 1987). Use of snapshot measurements of human disturbance (variables Tourism 1 and Tourism 2) did not significantly improve our results probably because administrative status of the WR (restricted touristic activities – see Methods) accounted for significant part of the touristic pressure (see Methods and Martinetto et al., 1998). The tendency of male’s vigilance to decrease with the number of groups of tourists might indicate a very local phenomenon of habituation as previously shown in this population by Martinetto et al. (1998) that reported no spatial and temporal avoidance of tourists by mouflon and lower flight distances of mouflon in frequented areas as compared to WR and in less frequented areas. It has also been shown in other mountain ungulates (alpine chamois, *Rupicapra r. rupicapra*, Gander and Ingold, 1997), that animals are able to get used to activities on trails as long as such recreational activities are regular and therefore predictable (Gossow et al., 1990; Hamr, 1988). However an apparent habituation may not mean that animals are not stressed. A study on American mouflon has shown that animals showing no vigilance behavior may still be considered stressed when taking into account their increased heart rate (Hayes, 1994). Moreover habituation may be costly because animals may be forced to stay in a disturbed area since there are no alternative sites nearby where they could take refuge and feed (Gill et al., 2001). Therefore this may indicate that habituation is not a psychological phenomenon where animals would acclimate to the human presence, but rather a physiological adaptation.

During the hunting period the level of vigilance in males was similar in WR and in HA. Two mutually non-exclusive explanations can be proposed. First, males were less philopatric than females, therefore males inhabiting the WR were less strictly restricted to this area than females (Dubois et al., 1996) and were therefore subject to the hunting pressure of neighboring areas. Further, male movements were exacerbated during the rutting period which almost fully matches the hunting period (Table 1). Secondly, the rut effect which was thus partly confounded with the hunting period may contribute to explain the similar level of vigilance among males belonging to the WR and the HA, and the absence of such an effect in females. This was also partly supported by the inclusion of the variable “rut” in most of the best selected models with AICc for males (Appendix A). During the rut, males increase vigilance in order to gather information about mating opportunities (Lung and Childress, 2007) and information related to dominance with other males (Bon et al., 1992). Support for such a hypothesis would then mean that social context overrides the role of human disturbance in shaping vigilance behavior.

For females our results are concordant with previous studies suggesting an increase in risk perception with reducing visibility (Humphries et al., 1990; Hayes, 1994 [heart rate]; Arenz and Leger, 1997), with thick vegetation reducing the probability of detection of an approaching predator (Desportes et al., 1987). For instance springboks are more vigilant in closed environment than in open ones (Bednekoff and Ritter, 1994). Moreover in our study area mouflon are subjected to effects of habitat closure. Open areas decreased 50% over the last 50 years (Garel et al., 2007). Probably in relation to this loss of open areas, mouflon have changed the composition of their diet by including a higher proportion of ligneous species compared to herbaceous species (Cransac et al., 1997). This diet shift could have caused the observed decrease in body growth. In addition, the reduction of high-visibility habitats might also contribute to affect mouflon growth by increasing risk effects (Risenhoover and Bailey, 1985). Thus as the level of stress increases (MacArthur et al., 1982), animals spend more time scanning their surroundings. Because of their larger body mass, males are expected to accept lower diet quality than females (Demment and Van Soest, 1985). This may lead to an increase in the time requested to process their food, and thus in the time available for the monitoring of their surroundings (Fortin et al., 2004; Blanchard and Fritz, 2007). Moreover, the fact that males are only affected by the quality of feeding sites and females are only influenced by visibility, supports the hypothesis that for females, predator detection is a priority, whatever the characteristics of the food patches (Ruckstuhl and Nehaus, 2002). Whereas for males, disturbance and foraging may be the driving factors influencing vigilance (Ruckstuhl and Nehaus, 2002; Benhaiem et al., 2008).

In agreement with our predictions, we underlined the effects of age on vigilance. Other studies have also supported that yearlings are less vigilant than adults (Arenz and Leger, 1997, 2000; Aviles and Bednekoff, 2007) because of the priority for growth and therefore, high food requirements, in early stages of life. A survey of the literature in Arenz and Leger

(2000) revealed that, of 22 mammalian species examined for an age effect on antipredator vigilance, juveniles were less vigilant than the adults in 11 species and in only 2 species they were more vigilant than adults. In the remaining nine, there were no differences, or the evidence was equivocal. For instance, in yellow-bellied marmots (*Marmota flaviventris*) the time allocated to wariness was to 87% in adults and 70% for yearling females (early morning) (Armitage and Corona, 1994). The lack of experience in research foraging may also explain this lower vigilance of yearlings as compared to adults. Juveniles must acquire skills in foraging, avoiding predators, interacting with conspecifics and have to learn to allocate their time efficiently to these activities (Sullivan, 1988).

Finally, we also reported an effect of female reproductive status. Females with young are generally more vigilant than non-reproductive females (in caribou Bergerud, 1974; in Alpine ibex, *Capra ibex ibex*, Toïgo, 1999; in elk Childress and Lung, 2003). As Rieucau and Martin (2008) for bighorn sheep, vigilance tactics differed between females without lamb and lactating females. They showed that lactating ewes relied solely on predator detection. In contrast, barren ewes benefited from both detection and dilution effects when group size increased and adjusted vigilance effort according to the proportion of lactating ewes in their group. Non-reproductive females may take advantage of the vigilance effort provided by reproductive females.

Our approach allowed us to investigate simultaneously the role of environmental, intrinsic and human factors in shaping vigilance patterns. In particular, in the context of management of populations, as for the Corsican mouflon population, our work should provide managers with valuable information on mouflon behavioral responses to human disturbances such as tourism and hunting, and to habitat characteristics (Dubray, 1988). Assessing what shapes the risk effects and understanding their consequences on population dynamics are essential requirements to ensure the conservation and the persistence of healthy populations and locally important economic activities (Gordon et al., 2004).

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Figures legends

Figure 1: (A) Location of the Caroux-Espinouse massif in France. (B) Digital elevation model of the range of the mouflon population in 1998 (thick plain line; altitude range: 118-1124m a.s.l.). Wildlife Reserve (two adjacent units; thin plain line) and the 5 transects sampled (dotted lines) were reported.

Figure 2: Representation of the best logistic model explaining adult male vigilance according to WR/hunting areas and period of hunting/no hunting (Table 2). Female estimates for a model including the same interaction than males (area status × hunting period) were reported for comparison. The estimates were associated with the level of “low quality feeding sites” for adult males, and with the level of “females with lamb” and the average of visibility in the home ranges for adult females. Squares for females and circles for males.

Table 1: table with different hypotheses and associated variables

Sources of variation in vigilance behavior	**Associated variables**	**Descriptions**
Human disturbance		
Touristic pressures	Tourism1	Number of group of tourists observed/hour (ranging from 0.03 to 2.96)
	Tourism2	Number of tourists observed/hour (ranging from 0.15 to 11.26)
Hunting period	Hunting	2 levels (March-August or September-November)
Area status	Area	2 levels (Wildlife Reserve or hunting and tourim areas)
Environmental characteristics		
Habitat visibility	Visibility	Continuous variable ranging from 18 pixels to 117 pixels
Quality of feeding sites	Feeding	2 levels (high quality or low quality feeding sites)
Social and individual characteristics		

Presence of horn in females	Horn	Binary variable (with or whitout horns)
Lambing periods in females	Lambing	2 levels (March-June or July-November)
Rutting period in males	Rut	2 levels (March-September or October-November)
Reproductive status	Repro	2 levels (female with lamb or female without lamb)
Reproductive composition of the group	Repro compF (for females)	3 levels (female with lamb or female without lamb in a reproductive group or female in a non-reproductive group)
	Repro compM (for males)	2 levels (male in a reproductive group or not)
Age	Age	2 levels (yearlings or adults)
Age composition of the group	Age comp	3 levels (yearlings only or yearlings with adults or adults alone)
Group size	Group size	Continuous variable ranging from 1 to 50 mouflon

Table 2: Generalized linear model (using a logit link) of vigilance rates in mouflon males, Caroux-Espinouse massif, France. The analysis of deviance table gives the effects of age, tourism, quality of feeding sites, mating season, group size, group composition, average visibility in the home range, hunting, WR and two-ways interactions on vigilance rates (see Table 1). Variables within brackets were evaluated concurrently to the preceding related variable (see Methods for details). Parameter values with its standard error are given for the best model (significant terms in bold). DF, degree of freedom and SE, standard error.

Vigilance Terms	Deviance	DF	p(X^2)
Full model: Age comp + Repro compM × Group size + Rut + Feeding + Tourism1 + Hunting x Area + Visibility			
Repro compM × Group size	0.892	2	0.640
Group size	0.029	1	0.864
Repro compM	1.266	2	0.531
Visibility	1.296	1	0.255
Rut	2.214	1	0.137
Tourism1	2.510	1	0.113
(Tourism2)	1.329	1	0.249
Age comp	7.808	2	0.020
(Age)	**5,740**	**1**	**0,017**
Feeding	**6.491**	**1**	**0.011**
Hunting × Area	**6.870**	**1**	**0.009**

Best model	Coefficient	SE
Intercept	-3.473	1.093
Yearling	-0.901	0.414
Feeding sites of low quality	1.910	1.022
Non-hunting season	-2.311	1.082
HA	-0.295	0.471
Non-hunting season.HA	2.411	1.125

Table 3: Generalized linear model (using a logit link) of vigilance rates in mouflon females, Caroux-Espinouse massif, France. The analysis of deviance table gives the effects of age, tourism, quality of feeding sites, horned female, group size, lambing season ,group composition, average visibility in the home range, hunting, WR and two-ways interactions on vigilance rates (see Table 1). Variables within brackets were evaluated concurrently to the preceding related variable (see Methods for details). Parameter values with its standard error are given for the best model (significant terms in bold). DF, degree of freedom and SE, standard error.

Vigilance Term	Deviance	DF	p(X^2)
Full model: Age + Repro compF × Group size + Lambing + Feeding + Tourism1 + Horn + Hunting × Area + Visibility			
Repro compF × Group size	0.321	2	0.852
Horn	0.691	1	0.406
Feeding	0.720	1	0.396
Hunting × Area	1.781	1	0.182
Group size	2.874	1	0.090
Hunting	2.674	1	0.102
Lambing	0.542	1	0.461
Visibility	**4.252**	**1**	**0.039**
Age	**4.975**	**1**	**0.026**
Repro compF	**9.990**	**2**	**0.007**
(Repro)	3.499	1	0,061
Area	**17.877**	**1**	**< 0.001**

Best model	Coefficient	SE
Intercept	-3.833	0.856
Yearling	-16.970	1657
Female without lamb in a reproductive group	-17.350	1700
Female with lamb	0.294	0.448
HA	2.439	0.756
Visibility	-0.015	0.007

SEs were not meaningful here because the fitted probabilities were extremely close to zero (Venables and Ripley, 2002; pgs. 197-198).

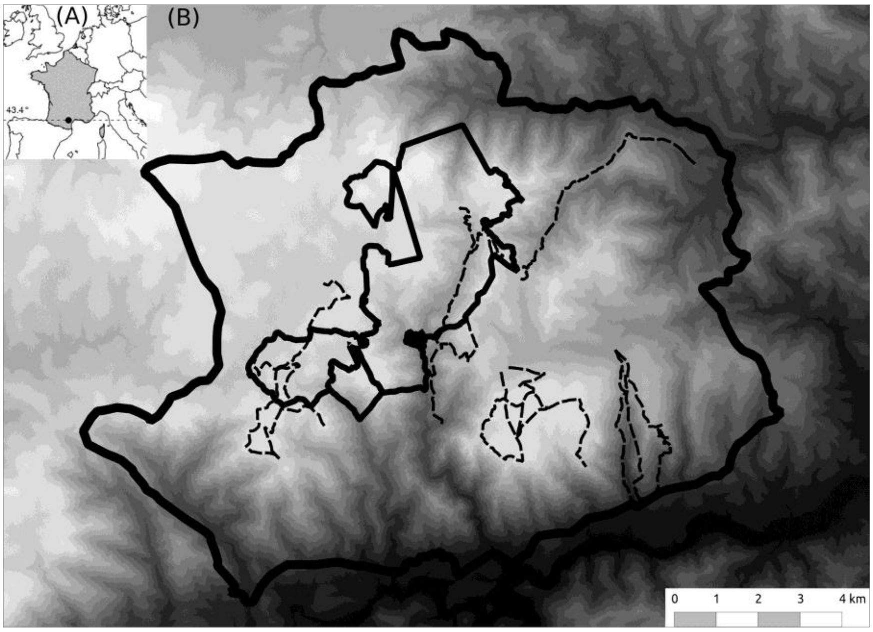

Fig. 1

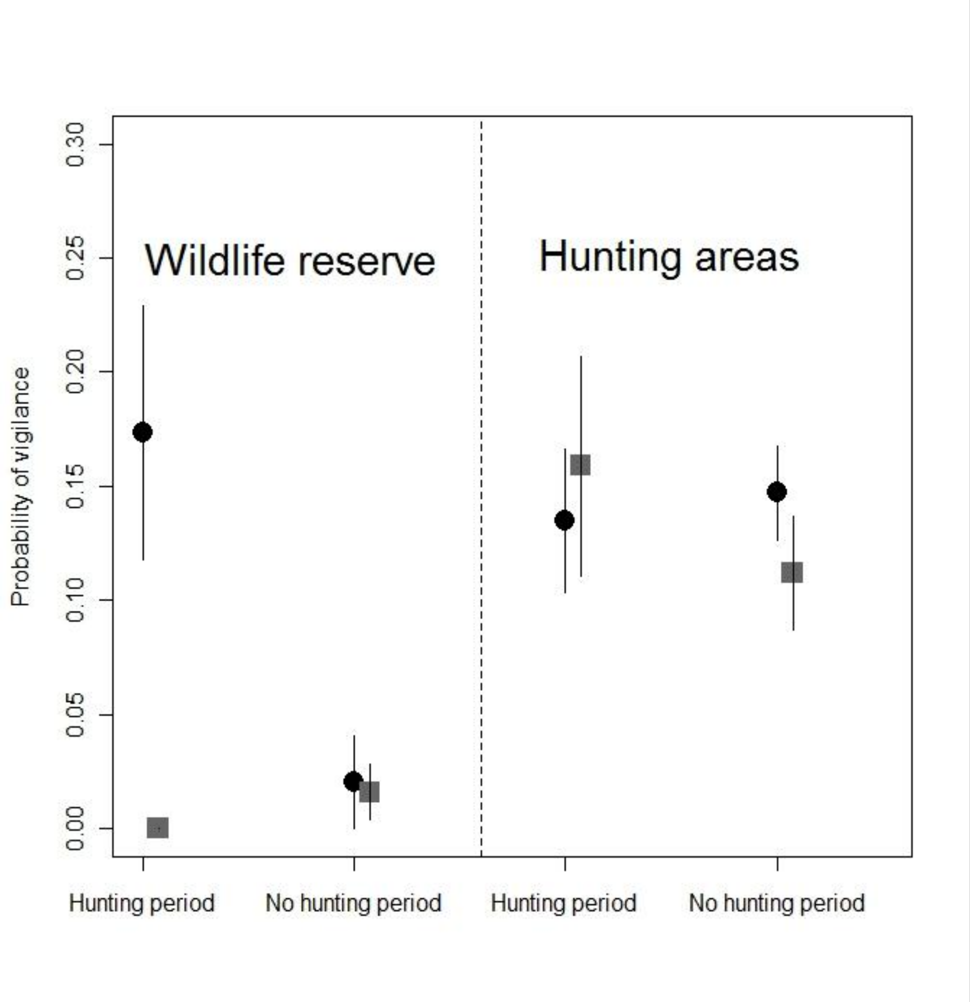
Wildlife reserve
Hunting areas
Probability of vigilance
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Hunting period
No hunting period
Hunting period
No hunting period

Fig. 2

APPENDIX A: MODEL SELECTION WITH AICc

(a) Logistic regression models explaining the variation in vigilance of male mouflon based on AICc. Only models with ΔAICc < 2 were reported.

Models	Age	Repro compM	Group size	Rut	Feeding	Tourism1	Hunting	Area	Visibility	Repro compM × Group size	Hunting × Area	AICc	ΔAICc	AICcw
m1	×			×	×	×	×	×			×	445,875	0,000	0,031
m2	×				×	×	×	×			×	446,072	0,198	0,028
m3	×				×		×	×			×	446,572	0,697	0,022
m4	×			×	×	×	×	×	×		×	446,658	0,784	0,021
m5	×			×	×		×	×			×	446,823	0,948	0,019
m6	×				×	×	×	×	×		×	447,126	1,251	0,017
m7	×		×	×	×	×	×	×			×	447,397	1,523	0,014
m8	×		×		×	×	×	×			×	447,552	1,678	0,013
m9	×	×		×	×	×	×	×			×	447,754	1,880	0,012

(b) Logistic regression models explaining the variation in vigilance of female mouflon based on AICc. Only models with ΔAICc < 2 were reported.

Models	Age	Repro compF	Group size	Horn	Lambing	Feeding	Tourism1	Hunting	Area	Visibility	Repro compF × Group size	Hunting × Area	AICc	ΔAICc	AICcw
m1	×	×	×						×	×			233,299	0,000	0,026
m2	×	×							×	×			233,907	0,607	0,020
m3	×	×	×		×			×	×	×			233,992	0,693	0,019
m4	×	×	×	×					×	×			234,263	0,964	0,016
m5	×	×	×		×			×	×	×		×	234,285	0,985	0,016
m6	×	×		×					×	×			234,446	1,147	0,015
m7	×	×	×		×				×	×			234,748	1,448	0,013
m8	×	×			×			×	×	×			234,800	1,500	0,013
m9	×	×	×					×	×	×			234,812	1,513	0,012
m10	×	×	×			×			×	×			234,994	1,695	0,011
m11	×	×	×				×		×	×			235,119	1,820	0,011
m12	×	×			×			×	×	×		×	235,151	1,852	0,010
m13	×	×	×					×	×	×		×	235,208	1,909	0,010

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