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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.

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; Thurfjell 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).

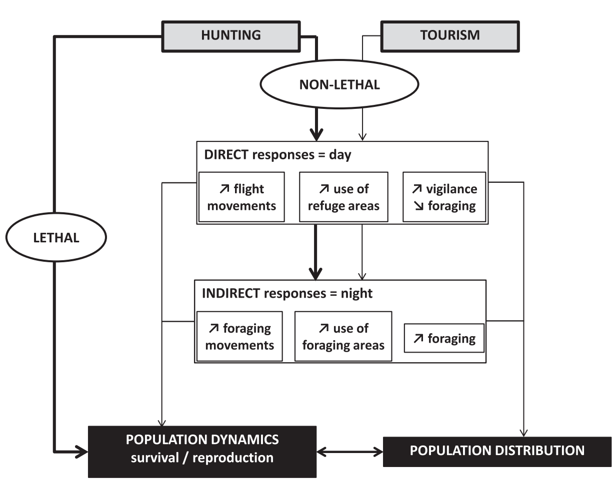

Fig. 1. Predictions concerning the direction of both direct and indirect behavioral responses expected from animals experiencing high tourism and/or hunting pressures. The theoretical framework and examples on which these predictions have been built are provided in Section 1. Larger arrows were used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

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; Thurfjell 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