Animal Behaviour 102 (2015) 169–187

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Coupling scale-specific habitat selection and activity reveals sex-specific food/cover trade-offs in a large herbivore

Pascal Marchand [a, b, *], Mathieu Garel [a], Gilles Bourgoin [c, d], Dominique Dubray [a], Daniel Maillard [a], Anne Loison [b]

[a] Office National de la Chasse et de la Faune Sauvage, Centre National d'Etudes et de Recherche Appliquée Faune de montagne, Juvignac, France
[b] Université de Savoie, Centre Interdisciplinaire des Sciences de la Montagne, CNRS UMR 5553, Laboratoire d'Ecologie Alpine, Le Bourget-du-Lac, France
[c] Université de Lyon, VetAgro Sup—Campus Vétérinaire de Lyon, Laboratoire de parasitologie vétérinaire, Marcy l'Etoile, France
[d] Université Lyon 1, CNRS UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, Villeurbanne, France

ARTICLE INFO

Article history:
Received 8 September 2014
Initial acceptance 8 October 2014
Final acceptance 19 December 2014
Published online
MS. number: 14-00723R

Keywords:
Caroux-Espinouse massif
foraging/ruminating-resting cycle
GPS
home range
Mediterranean mouflon
movement step
Ovis gmelini musimon × Ovis sp.
selection ratios
step selection functions

The balance between food and perceived predation risk has been revealed as one of the primary drivers of animal habitat selection. However, few studies have investigated how spatiotemporal scales and movement/activity patterns shape responses to this food/cover trade-off while accounting for individual characteristics (e.g. sex) and for variation in predation risk (e.g. hunting) and in resource abundance/quality. We hence studied temporal changes in habitat selection of 30 GPS-collared females and 15 males of Mediterranean mouflon, *Ovis gmelini musimon*×*Ovis* sp., at two scales, i.e. 48 h home range selection within a subpopulation area (broad scale) and choice of movement steps (defined as the linear segment between two consecutive locations) according to activity state (fine scale), in southern France. During the hunting-free/food-abundant period, males selected at both scales the foraging habitats providing the best conditions for optimizing their future reproductive success and only selected areas perceived as safe during inactive steps. During the corresponding lambing period, and at both scales, females selected areas perceived as safe that should optimize lamb survival. They switched to the best foraging habitats only when lambs were weaned and only for active steps. By contrast, during hunting, when food was also scarce, both sexes selected home ranges with high proportions of the habitats perceived as safe, in which they performed all their activities. This result suggested that risk avoidance exceeded all the other individual and environmental factors in the hierarchy of the determinants of habitat selection during the hunting period. Coupling scale-specific habitat selection and activity patterns was hence decisive in disclosing how individuals fulfil their specific needs under seasonally changing levels of habitat attributes important for fitness.

The analysis of how, when and why animals select particular habitats is a central issue in ecology. It has become crucial for conservation given that habitat loss and fragmentation have been identified as major threats to biodiversity (Fahrig, 2003; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Habitat selection is indeed not only the primary driver of population distribution but also contributes to individuals' survival and reproductive performance, and hence to population dynamics (Gaillard et al., 2010; Pulliam & Danielson, 1991).

Animals confronted with heterogeneous landscapes continuously assess the resources and conditions available in their surroundings. They should select the habitats allowing them to fulfil their internal needs and ultimately to ensure survival and reproduction (Hall, Krausman, & Morrison, 1997). Decisions taken at a given spatiotemporal scale may, however, depend on resources, environmental conditions, perceived predation risk and presence of conspecifics in the area chosen at broader scales. Habitat selection is hence a complex hierarchical decision-making process (Gaillard et al., 2010; Johnson, 1980; Morris, 1987; Senft et al., 1987) in which trade-offs are common. Indeed, foraging and protection attributes are rarely maximized in the same habitat type (Brown, 1999; Houston, McNamara, & Hutchinson, 1993; Lima & Dill,

* Correspondence: P. Marchand, Université de Savoie, Centre Interdisciplinaire des Sciences de la Montagne, CNRS UMR 5553, Laboratoire d'Ecologie Alpine, Bâtiment Belledonne Ouest, F-73376 Le Bourget-du-Lac, and Office National de la Chasse et de la Faune Sauvage, Centre National d'Etudes et de Recherche Appliquée Faune de montagne, 147 Route de Lodève, Les Portes du Soleil, F-34990 Juvignac, France.
E-mail address: pascal.marchand@univ-savoie.fr (P. Marchand).

http://dx.doi.org/10.1016/j.anbehav.2015.01.011
0003-3472/

1990). As an example, this pervasive food/cover trade-off has repeatedly been reported in empirical studies on large herbivores (e.g. red deer, *Cervus elaphus*: Mysterud & Ostbye, 1999; moose, *Alces alces:* Dussault et al., 2005).

The relative importance of each of the components of this trade-off may, however, vary with spatiotemporal scale, the most important factors in terms of fitness being expected to be selected at the highest scales (Rettie & Messier, 2000; Senft et al., 1987). Furthermore, habitat selection can also vary through time as resource quantity, quality and availability are dynamic, as well as other ecosystem characteristics (e.g. presence of predators or human activities). Again, scale is important, as selection criteria can vary at the interannual, seasonal and even within-day scales (night versus day; Godvik et al., 2009; McLoughlin, Wal, Lowe, Patterson, & Murray, 2011).

In addition to space and time, spatial behaviours should also depend on individuals' own traits (e.g. sex and age, Miquelle, Peek, & Van Ballenberghe, 1992) and states (e.g. reproductive status, Bjørneraas et al., 2011), which modify their energy requirements and their perception of or susceptibility to risk factors (Ruckstuhl and Neuhaus, 2006). The presence of an offspring at heel, and ultimately the need to ensure offspring survival, are, for example, common explanations for ungulate females selecting areas perceived as safe during the rearing period (bighorn sheep, *Ovis canadensis*: Festa-Bianchet, 1988; Stone's sheep, *Ovis dalli stonei*: Rachlow & Bowyer, 1998; fallow deer, *Dama dama*: Ciuti, Bongi, Vassale, & Apollonio, 2006; mountain goat, *Oreamnos americanus*: Hamel & Côté, 2007). This pattern, which is observed even in areas where natural predators have disappeared for a long time or in protected ones (e.g. Alpine ibex, *Capra ibex*: Grignolio, Rossi, Bertolotto, Bassano, & Apollonio, 2007), may be related to the long past evolution of species with natural predators (Byers, 1997).

In ruminant herbivores, an overlooked constraint on individuals at the daily level is imposed by their foraging and digestive features (Belovsky & Slade, 1986; Mysterud, 1998). Indeed, acquisition of energy can be decomposed into food searching, food acquisition and food processing (Cederlund, 1989; Hanley, 1982). The activity pattern of ruminants is consequently characterized by successive foraging and ruminating–resting bouts (Bourgoin et al., 2011; Gillingham, Parker, & Hanley, 1997; Pagon et al., 2013) that should influence which habitats are selected at the within-home range scale (Ager, Johnson, Kern, & Kie, 2003; Godvik et al., 2009; Mysterud, Larsen, Ims, & Ostbye, 1999). Fully exploring at which scale and how individuals with specific attributes adjust the balance between their ever-changing needs should allow researchers to decipher how populations are distributed in space in a dynamic context.

The increasing deployment of GPS technology and associated recording devices on animals ('biologgers', Ropert-Coudert and Wilson 2005), together with the development of GIS software and analytical methods, has greatly improved our ability to understand habitat selection patterns at multiple scales (Cagnacci, Boitani, Powell, & Boyce, 2010). Up to now, however, few studies on large terrestrial herbivores have combined information obtained from activity loggers and GPS locations (but see Bjørneraas et al., 2011; Ewald, Dupke, Heurich, Müller, & Reineking, 2014; Godvik et al., 2009; Van Moorter, Visscher, Jerde, Frair, & Merrill, 2010).

In this study, we aimed at determining how activity patterns influence habitat selection in males and females of a large herbivore, the Mediterranean mouflon, *Ovis gmelini musimon*×*Ovis* sp., in the Caroux-Espinouse massif, southern France. In this area, two of the main drivers of habitat selection, namely the 'predation' pressure (here, hunting) and food abundance/quality, vary strongly through time (contrast between a hunting and food-restricted period versus a nonhunting and food-abundant period; Fig. 1). We took advantage of the recent advances in GPS collars including head motion sensors allowing us to combine the analyses of activity data at the daily scale with location data at both daily and seasonal scales.

We hypothesized that factors determining habitat selection act as a hierarchical cascade from the home range to the within-home range scales (Fig. 1). At the top of the hierarchy, we expected the predominant factor to be risk avoidance when the risk of being killed is high and foraging in good-quality areas when the risk of being killed is low. The highest risk is during the hunting period, when food abundance and quality are low and the weather is generally inclement. We hence expected that the main habitats selected during this period should correspond to areas perceived as safe at all scales, for both males and females and irrespective of the activity level (Dussault et al., 2005; Herfindal et al., 2009; Mysterud & Ostbye, 1999). Even though food resources are senescent, autumn forage contributes to improving body condition before winter in large herbivores (Hurley et al., 2014), so that the baseline expectation in the absence of hunting would have been a selection for foraging areas. When disturbance and predation risks are low and forage is abundant and of high quality (spring and summer; no hunting), mouflon should select the habitat types providing the best foraging conditions at the home range scale. However, ungulate females with young offspring at heel have been consistently shown to trade off favourable foraging conditions with areas perceived as safe even in the absence of predators (e.g. Grignolio et al., 2007). Sex differences in habitat selection at the home range scale should therefore be greatest in spring with females favouring perceived risk avoidance over food before weaning and males expected to make the opposite choice. At a fine scale and for both sexes, habitat selection criteria were expected to be influenced by the foraging/ruminating–resting cycle. They should therefore differ between active and inactive phases (Bjørneraas et al., 2011; Godvik et al., 2009), with a selection of areas perceived as safe during resting/rumination bouts that may allow individuals to offset choices expected at a broader scale, in particular for males. Coupling analyses of activity level with fine and home range scale habitat selection allowed us to test the aforementioned hypotheses and to disclose the multiscale adjustments made by individuals when selecting habitats under different levels of perceived risk and foraging conditions.

METHODS

Study Site and Population

We collected data in the Mediterranean mouflon population inhabiting the Caroux-Espinouse massif (43°38′N, 2°58′E, 17 000 ha, 150–1124 m above sea level), in southern France (Fig. 2). The study site was characterized by a Mediterranean climate with both oceanic and mountainous influences (Baudière, 1962). Droughts often happened during the summer (Garel, Loison, Gaillard, Cugnasse, & Maillard, 2004) whereas snowfalls during winter were often limited to plateaux and variable from year to year.

Since 1973, hunting has been the main source of regulation for this population. It has also involved behavioural and life history consequences for mouflon (Benoist, Garel, Cugnasse, & Blanchard, 2013; Garel et al., 2007; Marchand et al., 2014). During the study period (2003–2010), hunting occurred from 1 September to the end of February. On average 378 (SD = 109) animals were harvested per year (out of probably more than 2500 individuals; Marchand et al., 2014), evenly distributed between both sexes. Driven hunts with hounds were carried out on Wednesdays, Saturdays, Sundays and public holidays, target species being wild boar, *Sus scrofa scrofa*,