



## Do ecologically close species shift their daily activities when in sympatry? A test on chamois in the presence of mouflon

GAËLLE DARMON<sup>1,2\*</sup>, GILLES BOURGOIN<sup>2,3</sup>, PASCAL MARCHAND<sup>1,4</sup>, MATHIEU GAREL<sup>4</sup>, DOMINIQUE DUBRAY<sup>4</sup>, JEAN-MICHEL JULLIEN<sup>4</sup> and ANNE LOISON<sup>1</sup>

<sup>1</sup>Laboratoire d'écologie Alpine CNRS UMR5553, Université de Savoie, Bâtiment Belledonne, Le Bourget-du-Lac F-73376, France

<sup>2</sup>CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, Université de Lyon, F-69000, Lyon, Université Lyon 1, Villeurbanne F-69622, France

<sup>3</sup>VetAgro Sup – Campus Vétérinaire de Lyon, Université de Lyon, F-69000, Lyon, 1 avenue Bourgelat, Marcy l'étoile 69280, France

<sup>4</sup>Office National de la Chasse et de la Faune Sauvage, Centre National d'étude et de Recherche Appliquée Faune de Montagne, 147 Route de Lodève, Les Portes du Soleil, Juvignac F-34990, France

Received 6 September 2013; revised 17 November 2013; accepted for publication 18 November 2013

Temporal partitioning of daily activities between species may promote coexistence within animal communities by reducing behavioural interference, particularly when species highly overlap in the use of space and resources. Such a strategy may be used by Alpine chamois (*Rupicapra rupicapra rupicapra*) when in the presence of mouflon (*Ovis gmelini musimon* × *Ovis* sp.), an introduced highly gregarious species with a broader ecological niche, overlapping with that of chamois. Using simultaneous monitoring of 29 Global Positioning System-collared chamois and 12 mouflon, we assessed the temporal variation in activity patterns of chamois amongst two subpopulations: one without mouflon and one with mouflon, during January and August, which are the two most extreme periods of spatial overlap of mouflon with chamois distribution. Substantial differences in activity patterns between chamois and mouflon were observed (mean  $13.8 \pm 10.5\%$  in January and  $10.6 \pm 11.6\%$  in August). More subtle differences appeared between both subpopulations of chamois and persisted, regardless of the spatial overlap with mouflon ( $3.2 \pm 1.8\%$  in January and  $2.6 \pm 1.5\%$  in August), thus highlighting that there is no behavioural interference from mouflon on chamois. Our findings suggest that the temporal partitioning of daily activities between chamois and mouflon, although probably a result of species-specific adaptations to environmental conditions, may contribute to their coexistence. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 621–626.

**ADDITIONAL KEYWORDS:** animal community – coexistence – interference competition – large herbivores – mountain – niche overlap – time partitioning.

### INTRODUCTION

Understanding the mechanisms allowing coexistence between species constitutes a major challenge in community ecology, particularly when studying ecologically close species (i.e. species highly overlapping

in space and resource use). To coexist, co-occurring species should indeed differ with respect to at least one dimension of their ecological niche (*sensu* Hutchinson, 1957): space, habitat resources, and/or time (limiting similarity theory, MacArthur & Levins, 1967). When ecologically close species highly overlap in space, they may interact directly (e.g. through aggressive behaviours or occupation of the patches;

\*Corresponding author. E-mail: darmon\_gaelle@yahoo.fr

Case & Gilpin, 1974; Kronfeld-Schor & Dayan, 2003). Although less studied than exploitative competition, such behavioural interference could be an important structuring driver of animal communities (Case & Gilpin, 1974; Amarasekare, 2002).

Understanding how species adjust their behaviour to avoid interference in large herbivore communities has biological and management implications (Vázquez, 2002), especially because of an ongoing increase of interactions between native and non-native species with similar ecological requirements (Loison, Toïgo & Gaillard, 2003). In particular, larger and more gregarious species often lead smaller and less gregarious species to adjust their behaviour to avoid behavioural interference (Forsyth, 2000; Valeix, Chamaillé-Jammes & Fritz, 2007; Ferretti, Sforzi & Lovari, 2011), through spatial adjustment (Ferretti *et al.*, 2011; Macandza, Owen-Smith & Cain, 2012) or the use of suboptimal resources (Chirichella, Ciuti & Apollonio, 2013). Besides these segregations on the spatial and the habitat dimensions of ecological niches (Tokeshi, 1999), species may shift their daily activities to reduce behavioural interference (Kronfeld-Schor & Dayan, 2003). However, such a response through temporal segregation has been investigated to a lesser extent in large herbivores (Valeix *et al.*, 2007).

In the present study, we investigated the daily activity pattern of a native species, the Alpine chamois (*Rupicapra rupicapra rupicapra*), in the presence of an introduced species, the mouflon (*Ovis gmelini musimon* × *Ovis sp.*), a species of similar body size (in the range 35–50 kg for females and males of both species; Catusse *et al.*, 1996), in the northern French Alps. The previously observed high spatial and ecological overlap between chamois and mouflon (88% of similarity between the niches; Darmon *et al.*, 2012) may favour the potential for competition between these two species. Because chamois form smaller and spatially unstable groups compared to mouflon (Darmon *et al.*, 2007, 2012) and can be limited by resources in our population (density-dependence in juvenile body mass of chamois; Garel *et al.*, 2011), chamois may suffer from behavioural interference by mouflon, as suggested in the Italian Alps (Chirichella *et al.*, 2013). We assessed whether temporal partitioning may be an efficient strategy employed by chamois to avoid behavioural interference.

We expected a high temporal overlap in activity patterns between chamois and mouflon because of similar activity rhythms (Rüttimann, Giacometti & McElligott, 2008; Bourgoïn *et al.*, 2011) induced by similar energetic and ecological needs (Hofmann, 1989; Bertolino, Di Montezemolo & Bassano, 2009; Marchand *et al.*, 2013) (H1). As a result of this temporal overlap, chamois living sympatrically with

mouflon should shift their peak of activity towards periods when mouflon are inactive to reduce behavioural interference from mouflon (H2). Owing to the continuous recording of motion data from 41 Global Positioning System (GPS) collars fitted on both chamois and mouflon, we compared daily activity patterns of chamois and mouflon, and then of two subpopulations of chamois: one living allopatrically and one living sympatrically with mouflon.

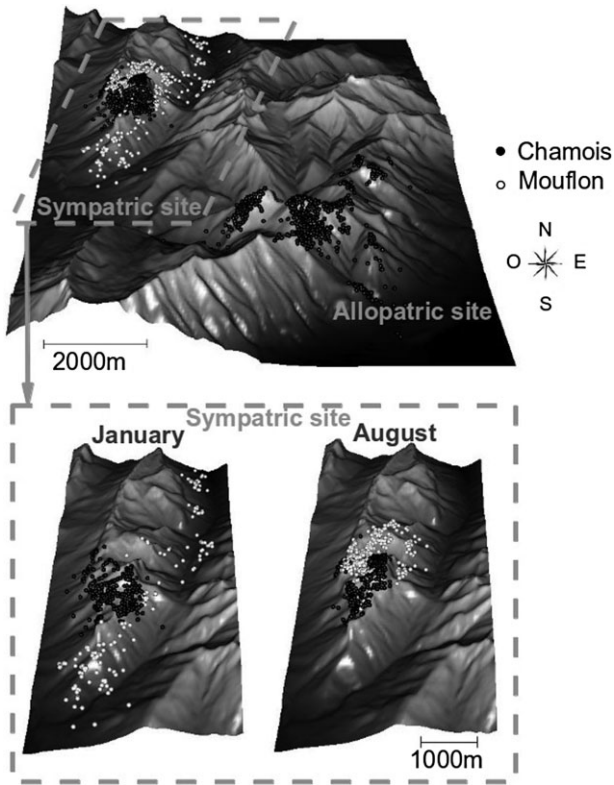
## MATERIAL AND METHODS

### STUDY SITES

The study was conducted in the Bauges Game and Wildlife National Reserve (northern Alps, France, 45.65°N, 6.23°E, 5205 ha, 600–2217 m a.s.l.). Although chamois are endemic to the study site, mouflon were introduced in the 1950s and are now the second most abundant ungulate species after chamois (Darmon *et al.*, 2012). We considered two spatially close chamois subpopulations (approximately 9 km apart) experiencing similar environmental conditions (Duparc *et al.*, 2012): Armene, where chamois lived in allopatry ('allopatric site'), and Pleuven, where they lived in sympatry with mouflon ('sympatric site'). On average, 57 chamois km<sup>-2</sup>, and 51 chamois and 23 mouflon km<sup>-2</sup>, respectively, were censused in Armene and Pleuven from June to October 2004 and 2005 (Darmon, 2007) (Fig. 1). During our study period, from 2004 to 2009, chamois and mouflon had no natural predators and almost no interactions with other wild ungulates occupying lower elevation ranges (roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, and wild boar *Sus scrofa*). Domestic cows *Bos taurus* occupied high elevation pastures a hundred days in summer from 2003 in Armene and from 2007 in Pleuven but, being enclosed, direct contacts with chamois and mouflon were limited.

### ACTIVITY DATA

We trapped 29 chamois (16 females in the sympatric site and 13 females in the allopatric site) and 12 mouflon (including two young males) during spring–summer 2004–2009 using falling nets baited with salt licks (Jullien, Pépin & Marouze, 2001). Animals were fitted with GPS collars Lotek 3300S (Engineering Inc.), which recorded one location day<sup>-1</sup> at 07.00 h (local time) for the collars deployed until 2007 and at least one location/20 min for 2 days of the week before 2007 and every day after 2007. Activity sensors on the collars recorded motion data (i.e. animals' head movements) every 5 min every day via two perpendicular captive-ball tilt switches (mean ± SD recording time: 403 ± 141 days).



**Figure 1.** Three-dimensional spatial distribution of all individuals (top left), and of chamois and mouflon, in the sympatric site (shaded square) represented on the elevation map (range 600–2217 m). The spatial overlap of mouflon on chamois was minimal in January [6% of 319.08 ha (2090.73 ha occupied by both species)] and maximal in August [34% of 245.79 ha (492.67 ha occupied by both species)].

#### STATISTICAL ANALYSIS

To predict the activity state (active versus inactive) of mouflon, we applied the discriminant model developed by Bourgoïn *et al.* (2011) to motion data. The similar model for chamois, calibrated from visual observations of three free-ranging collared chamois (73- and 45-min periods of complete activity and inactivity, respectively; Bourgoïn *et al.*, 2011) classified individuals as active or inactive with a success rate of 94.3% [95% confidence interval (CI) = 83.8–100.0] and 96.0% (95% CI = 88.0–100.0), respectively. We applied this model to predict the activity state of each marked chamois.

To test the influence of mouflon on chamois activity pattern, we first selected the two most contrasted months during which direct interactions of chamois with mouflon were minimum and maximum (i.e. minimum and maximum overlap of mouflon on chamois distribution). Considering one location per day (all daily locations and a random daily location

among the repeated daily recordings), we calculated the spatial overlap of mouflon on chamois distribution by measuring the proportion of chamois home ranges occupied by mouflon home ranges (95% kernels with *ad hoc* smoothing parameters). The two months for which the largest difference in spatial overlap was observed were January (lowest spatial overlap: 6% of the 319.1 ha used by chamois) and August (highest spatial overlap: 34% of 245.8 ha used by chamois). We then performed month-specific analyses using generalized additive mixed models (Pinheiro & Bates, 2000) with the mean proportion of time that an individual was active per hour (pA) as the response variable, and animal identity and year as random effects. The baseline model (M0) included hour as a smoothed term with a cubic regression spline to ensure the estimations of pA at midnight were adjusted (i.e. head and tail of the curve) as the activity pattern is cyclic daily. To respectively address hypotheses H1 (similar activity patterns between the two species) and H2 (different activity patterns between chamois of the two subpopulations), we considered a model (M1) accounting for a ‘species’ effect (two levels: chamois and mouflon) and a full model (M2) accounting for a ‘species-site’ effect (three levels: mouflon, chamois in sympatry, chamois in allopatry) with specific smoothed terms for each level of the factors. We compared the three models using differences in Akaike information criterion corrected for small sample size ( $\Delta\text{AICc}$ ). We then computed the percentage of explained deviance by models M1 and M2 compared to M0 (Table 1). Finally, we computed the hourly differences in predicted pA between the chamois and mouflon (from model M1) and between the two chamois subpopulations (from model M2) for each month and compared these differences between months using Wilcoxon *t*-tests. Analyses were performed using R, version 2.14.1 (R Development Core Team, 2011) with the packages *adehabitat* (Calenge, 2006), *MASS* (Venables & Ripley, 2002), and *gamm4* (Wood, 2006).

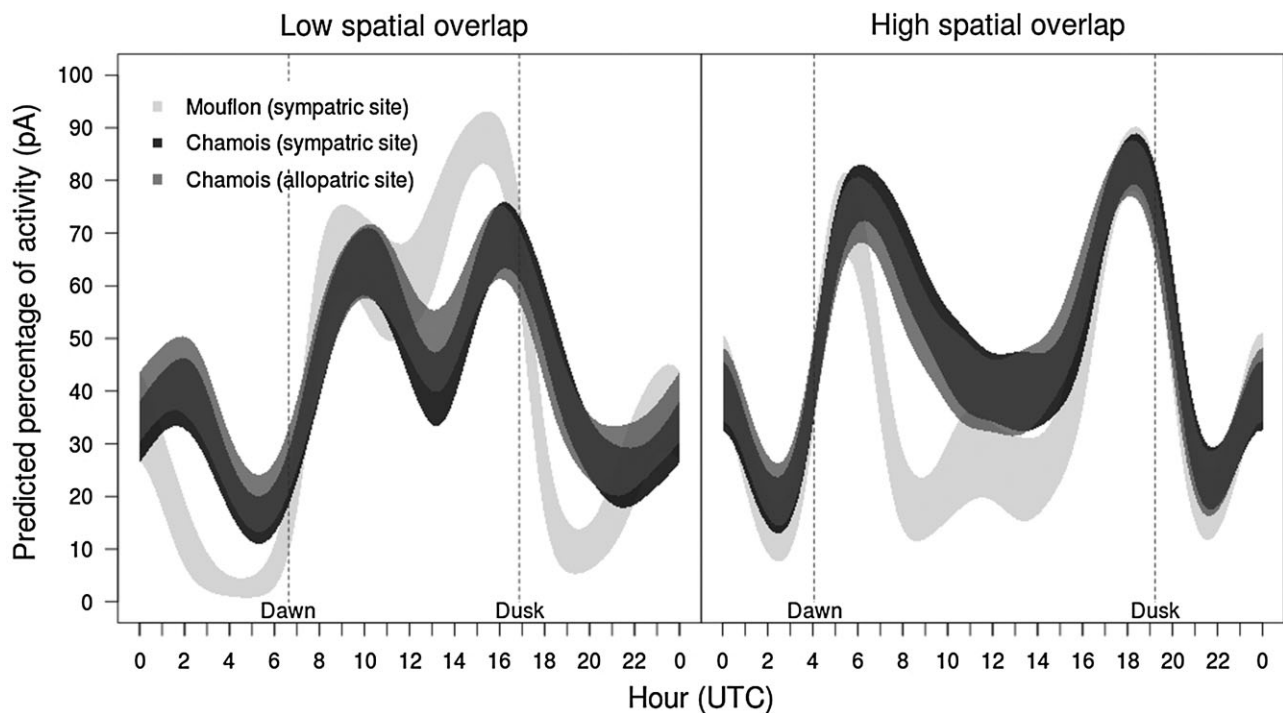
#### RESULTS

The hypothesis H1 was partially validated because both species showed a bimodal activity pattern with peaks early in the morning and late in the evening, although marked differences in activity patterns (i.e. level and time of activity) appeared between them (‘species’ effect) in both months [mean  $\pm$  SD = 13.8  $\pm$  10.5% (January); 10.6  $\pm$  11.6% (August) with no significant difference between the two months, Wilcoxon *t*-test: *P*-value = 0.24] (Fig. 2, Table 1). Although models M2 outperformed models M1 both during the period of high and low spatial overlap, the consideration of a distinction between the two subpopulations of chamois (within the ‘species-site’ effect) had

**Table 1.** Comparison of the models predicting individual mean proportion of hourly activity for each month: contribution of ‘species’ effect (model M1) compared to the baseline model (M0, details in the text) and of ‘species-site’ effect (model M2) compared to M1

	Contribution of ‘species’ effect compared to baseline model		Contribution of ‘species-site’ effect compared to ‘species’ effect	
	$\Delta AIC_{C_{M0-M1}}$	$\frac{\Delta \text{Deviance}_{M0-M1}}{\text{Deviance}_{M0}}$	$\Delta AIC_{M1-M2}$	$\frac{\Delta \text{Deviance}_{M1-M2}}{\text{Deviance}_{M1}}$
January (low spatial overlap)	11009	37.8%	197	0.7%
August (high spatial overlap)	4456	27.8%	203	1.3%

AIC, Akaike information criterion; AICc, corrected AIC.



**Figure 2.** Daily activity patterns of chamois in allopatry, of chamois in sympatry with mouflon, and of mouflon, in January when the spatial overlap of mouflon on chamois was minimal (6% of 319.08 ha; left) and in August, whereas it was maximal (34% of 245.79 ha; right). The thickness of the curves corresponds to the predicted value ( $\pm$  SE). UTC, coordinated universal time.

a much smaller influence on model fit than the ‘species’ effect (Table 1). By contrast to H2, the hourly differences in predicted pA between the two sub-populations of chamois were low, regardless of the spatial overlap with mouflon ( $3.2 \pm 1.8\%$ ;  $2.6 \pm 1.5\%$ ) and not significant between the two months (Wilcoxon *t*-test: *P*-value = 0.21), thus highlighting no shift in chamois activity pattern when overlap with mouflon increases in the sympatric site.

## DISCUSSION

Although both chamois and mouflon showed activity peaks early in the morning and late in the evening in both months, as typically observed in large herbivores (Cederlund, 1989), substantial differences in daily activity patterns appeared between these two species (Fig. 2). Because chamois are more sensitive to the availability of forage quality than mouflon (Hofmann,



1989; Bertolino *et al.*, 2009), their higher activity level during daytime in summer is likely to reflect movements required to select high quality patches. For mouflon, activity levels emphasize the higher sensitivity of the species to extreme temperatures compared to chamois because they decreased more during the thermally stressing hours (i.e. night in winter and day in summer; Bourgoïn *et al.*, 2011). The differences in activity patterns between chamois and mouflon suggest species-specific endogenous rhythms (foraging/ruminating, Hofmann, 1989) or sensitivity to environmental constraints (e.g. thermoregulation; Bourgoïn *et al.*, 2011).

Despite a large temporal overlap between chamois and mouflon activity patterns, almost no differences in activity patterns between chamois in the allopatric site and chamois in the sympatric site occurred and persisted, regardless of the spatial overlap between the two species, therefore highlighting that there is no behavioural interference by mouflon in the sympatric site. In the Swiss Alps, Rüttimann *et al.* (2008) did not find any behavioural interference either between domestic sheep *Ovis aries* and chamois. These findings suggest a non-competitive coexistence between chamois and mouflon (Tokeshi, 1999), possibly because of the high availability of resources for adult chamois when their spatial overlap was high. A shift in chamois activities in the presence of mouflon may not be necessarily involved because different species-specific daily activity patterns appear to be involved in limiting behavioural interference. However, behavioural interference has repeatedly been suggested in large herbivore communities, often induced by non-native species on native species (Chirichella *et al.*, 2013). Susceptibility to behavioural interference may depend on various factors, such as sex (Hamr, 1988; Ferretti *et al.*, 2011), body size (Valeix *et al.*, 2007; Ferretti *et al.*, 2011), gregariousness and density (Forsyth & Hickling, 1998; Ferretti *et al.*, 2011), or external disturbances such as predators (Eriksen *et al.*, 2011) or human activities (Hamr, 1988). In addition, interspecific spatial overlap on fundamental habitat resources, such as food patches, may lead to stronger potential for interference. Also, other mechanisms to avoid interference would lead species to locally adjust their spatial distribution (Ferretti *et al.*, 2011; Macandza *et al.*, 2012) or their selection of resources in the presence of a direct competitor (Chirichella *et al.*, 2013) rather than shift their daily activities. Considering a global approach merging spatial, habitat resources, and temporal dimensions of ecological niches could deepen our knowledge about the mechanisms of avoidance of behavioural interference between ecologically close species.

## ACKNOWLEDGEMENTS

All of the experiments were performed in compliance with current French laws on wildlife and animal welfare. We wish to thank O. Bantus, M. Henriques, and W. Renaud (Lotek Wireless Inc.) for technical support, as well as all the volunteers who participated in the captures. We are also grateful to C. Plasse, A. Darlington, J. A. Allen, N. Owen-Smith, F. Ferretti, B. P. Kutler, and the two anonymous reviewers for their useful comments.

## REFERENCES

- Amarasekare P. 2002.** Interference competition and species coexistence. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 2541–2550.
- Bertolino S, Di Montezemolo NC, Bassano B. 2009.** Food-niche relationships within a guild of alpine ungulates including an introduced species. *Journal of Zoology* **277**: 63–69.
- Bourgoïn G, Garel M, Blanchard P, Dubray D, Maillard D, Gaillard JM. 2011.** Daily responses of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) activity to summer climatic conditions. *Canadian Journal of Zoology* **89**: 765–773.
- Calenge C. 2006.** The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**: 516–519.
- Case TJ, Gilpin ME. 1974.** Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America* **71**: 3073–3077.
- Catusse M, Corti R, Cugnasse JM, Dubray D, Gibert P, Michallet J. 1996.** *La grande faune sauvage de montagne*. Paris: ONC- Hatier.
- Cederlund G. 1989.** Activity patterns in moose and roe deer in a north boreal forest. *Ecography* **12**: 39–45.
- Chirichella R, Ciuti S, Apollonio M. 2013.** Effects of livestock and non-native mouflon on use of high-elevation pastures by Alpine chamois. *Mammalian Biology* **78**: 344–350.
- Darmon G. 2007.** Influence des interactions interspécifiques sur l'utilisation de l'habitat par les ongulés sauvages: cas du chamois et du mouflon dans le massif des Bauges. PhD Thesis, University Lyon 1.
- Darmon G, Calenge C, Loison A, Jullien JM, Maillard D, Lopez JF. 2012.** Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography* **35**: 45–53.
- Darmon G, Calenge C, Loison A, Maillard D, Jullien JM. 2007.** Social and spatial patterns determine the population structure and colonisation processes in mouflon. *Canadian Journal of Zoology* **85**: 634–643.
- Duparc A, Redjadj C, Viard-Créat F, Lavorel S, Austrheim G, Loison A. 2012.** Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. *Applied Vegetation Science* **16**: 305–316.
- Eriksen A, Wabakken P, Zimmermann B, Andreassen HP, Arnemo JM, Gundersen H, Liberg O, Linnell J,**

- Milner JM, Pedersen HC. 2011.** Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. *Animal Behaviour* **81**: 423–431.
- Ferretti F, Sforzi A, Lovari S. 2011.** Behavioural interference between ungulate species: roe are not on velvet with fallow deer. *Behavioral Ecology and Sociobiology* **65**: 875–887.
- Forsyth DM. 2000.** Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. *Journal of Zoology* **252**: 215–225.
- Forsyth DM, Hickling GJ. 1998.** Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition. *Oecologia* **113**: 377–382.
- Garel M, Gaillard JM, Jullien JM, Dubray D, Maillard D, Loison A. 2011.** Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *Journal of Mammalogy* **95**: 1112–1117.
- Hamr J. 1988.** Disturbance behaviour of chamois in Alpine tourist area of Austria. *Mountain Research and Development* **8**: 65–73.
- Hofmann RR. 1989.** Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* **78**: 443–457.
- Hutchinson GE. 1957.** Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* **22**: 415–427.
- Jullien JM, Pépin G, Marouze E. 2001.** La cham'arce, un filet pour la capture des ongulés de montagne. *Faune Sauvage* **254**: 16–21.
- Kronfeld-Schor N, Dayan T. 2003.** Partitioning of time as an ecological resource. *Annual Review of Ecology Evolution and Systematics* **34**: 153–181.
- Loison A, Toïgo C, Gaillard JM. 2003.** Large herbivores in European Alpine ecosystems: current status and challenges for the future. In: Nagy L, Grabherr G, Körner C, Thompson DBA, eds. *Alpine biodiversity in Europe*. Berlin: Springer, 341–366.
- Macandza VA, Owen-Smith N, Cain JW III. 2012.** Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* **121**: 891–898.
- MacArthur R, Levins R. 1967.** The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**: 377–385.
- Marchand P, Redjadj C, Garel M, Cugnasse JM, Maillard D, Loison A. 2013.** Are mouflon (*Ovis gmelini musimon*) really grazers? A review of variation in the composition of their diet. *Mammal Review* **43**: 275–291.
- Pinheiro JC, Bates DM. 2000.** *Mixed-effects models in S and S-PLUS*. New York: Springer Verlag.
- R development core team. 2011.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rüttimann S, Giacometti M, McElligott AG. 2008.** Effect of domestic sheep on chamois activity, distribution and abundance on sub-alpine pastures. *European Journal of Wildlife Research* **54**: 110–116.
- Tokeshi M. 1999.** *Species coexistence: ecological and evolutionary perspectives*. Cambridge: Blackwell Science.
- Valeix M, Chamaillé-Jammes S, Fritz H. 2007.** Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia* **153**: 739–748.
- Vázquez DP. 2002.** Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological Invasions* **4**: 175–191.
- Venables WN, Ripley BD. 2002.** *Modern applied statistics with S*. New York, NY: Springer.
- Wood S. 2006.** *Generalized additive models: an introduction with R*. Boca Raton, FL: CRC Press.