

REVIEW

Are mouflon *Ovis gmelini musimon* really grazers? A review of variation in diet composition

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ABSTRACT

1. We reviewed data on the diets of mouflon (Mediterranean island populations *Ovis gmelini musimon* and introduced hybridized populations *Ovis gmelini musimon* × *Ovis* sp.) from 33 field studies (comprising 51 independent data points suitable for analysis) to detect general patterns in the botanical composition of the diet and identify ecological factors explaining its variation. We expected mouflon, generally classified as grazers, to include botanical entities other than grass in their diet, especially when they are forced to do so by low resource availability, and in certain seasons.

2. Diet composition was investigated based on samples of rumen content and faeces. We combined these data with environmental characteristics at each site using a co-inertia analysis.

3. As expected, grass often constituted the highest proportion in the diet (in 28 of the 51 data points) and represented on average 35% (range = 0–91%) of mouflon diet, confirming the importance of this food for the species. However, referring strictly to commonly used thresholds (>75% or >90%) shows that the classification of mouflon as grazers could be questioned. Indeed, forbs and shrubs constituted 24% (range: 0–93%) and 16% (range: 0–55%) of their diet, respectively, so that mouflon should at least be considered as variable grazers. Forbs represented a high percentage of the overall diet in the Kerguelen Archipelago, southern Indian Ocean (autumn and winter: 73%) and Teide National Park, Canary Islands, Spain (autumn and winter: 83%), whereas shrubs represented a high proportion of the overall diet in Mediterranean areas (19%).

4. Diet composition varied with spatio-temporal variation in forage availability (documented as habitat related or seasonal variation), confirming that mouflon are able to feed on a large variety of plants.
5. Further investigations concerning both digestive morphology and consequences of the inclusion of browse in the diet on population dynamics of mouflon are needed to understand the persistence of this species over a wide range of habitats despite a potential mismatch between its digestive ability and its observed diet.

INTRODUCTION

Large herbivore species are traditionally classified according to their diet into three distinct categories, depending on their relative consumption of grass and browse: grazers, browsers, and mixed or intermediate feeders (Hofmann 1989). However, this classification is often based not only on diet composition but also on digestive system morphology and physiology. Rumen morphophysiology is particularly variable among ruminants (Hofmann 1989 and references therein), and the degree to which their rumen contents stratify (and morphophysiological adaptations related to this) is related to their ability to digest grass and browse (Clauss et al. 2010). Discovering how digestive morphophysiology actually constrains diet in the wild is essential to understanding how herbivores impact vegetation in natural landscapes (Duncan & Poppi 2008, Prins & Fritz 2008) and is the topic of active research combining ecophysiology and comparative studies (e.g. Pérez-Barberia & Gordon 1999, Pérez-Barberia et al. 2001a, 2004, Codron & Clauss 2010). Clauss et al. (2010) recently suggested that the classifications should be clearly distinguished: the terms 'moose type' and 'cattle type' should be used to contrast rumen with different morphophysiological features (Clauss et al. 2009a); the terms 'grazer', 'browser' and 'intermediate feeder' should only be used for classification based on diet composition. Following this principle, the extreme 'grazer' and 'browser' categories could be used to describe species consuming >75% (Pérez-Barberia & Gordon 1999, Pérez-Barberia et al. 2001b, Mendoza et al. 2002) or >90% (Janis 1990, Pérez-Barberia et al. 2001a) of grasses and browse, respectively. Studies focusing on diet composition and (i) covariation with digestive morphophysiology (Clauss et al. 2009a), (ii) interspecific comparisons (Van Wieren 1996) and (iii) intraspecific variability (Cornelis et al. 1999, Gebert & Verheyden-Tixier 2001) suggest that the plasticity in diet composition differs depending on whether a species is at the moose-type/browser or the cattle-type/grazer end of the classification and that obligate grazers seem to be rarer than obligate browsers (e.g. Gagnon & Chew 2000, Codron et al. 2007 in African ungulates). However, general conclusions have been hampered by the lack of diet studies at the

intraspecific level and in different ecological contexts for most wild species. Analysis of variation in diet composition and factors determining variation offers a unique opportunity to assess whether new threats to species could be posed by global changes (climate warming and land use changes, e.g. areas being colonized by shrubs and forests, see Garel et al. 2007).

Within Hofmann's grazer/browser classification, Mediterranean mouflon *Ovis gmelini musimon* (*sensu* Cugnasse 1994, also named European mouflon *Ovis aries musimon*) have been classed as grazers (Geiger et al. 1977) based on both their digestive morphophysiology (Kamler 2001, Behrend et al. 2004) and the importance of grass in their diet (García-González & Cuartas 1989, Faliu et al. 1990, Homolka 1993, Cransac et al. 1997). From a neolithic origin in Mediterranean islands (Cyprus, Sardinia and Corsica), mouflon have been introduced to diverse habitats over a wide geographical area (Fig. 1, Table 1 and Appendix S1), often to increase local diversity of wild game species, after variable levels of hybridization with wild and domestic ovines (Uloth 1972, Cugnasse 1994). Mouflon have been forced to face habitats ranging from polar tundra in sub-Antarctic islands to continental forests of central Europe, i.e. habitats distinct from those in which this species originally evolved (Rezaei et al. 2010). Mouflon are therefore a relevant study species to test the extent to which (and the circumstances under which) they modify their diet composition to include botanical entities other than grass. The number of diet studies performed (Table 1 and Appendix S1) now allows a comparative review of mouflon diets. In addition, mouflon introductions have raised issues of competition with native species (Bertolino et al. 2009) and of impacts on ecosystems (e.g. forestry: Homolka 1993, Babad 1997; island biodiversity: Chapuis et al. 1994, Garzón-Machado et al. 2010), which have been poorly studied and would benefit from a better understanding of the determinants of the variation in mouflon diet.

We review the findings from 33 studies of mouflon diet in order to (i) identify the common patterns in diet composition, (ii) evaluate variation in diet and determine which ecological factors best explain such variation and (iii) reappraise the classification of mouflon as grazers.

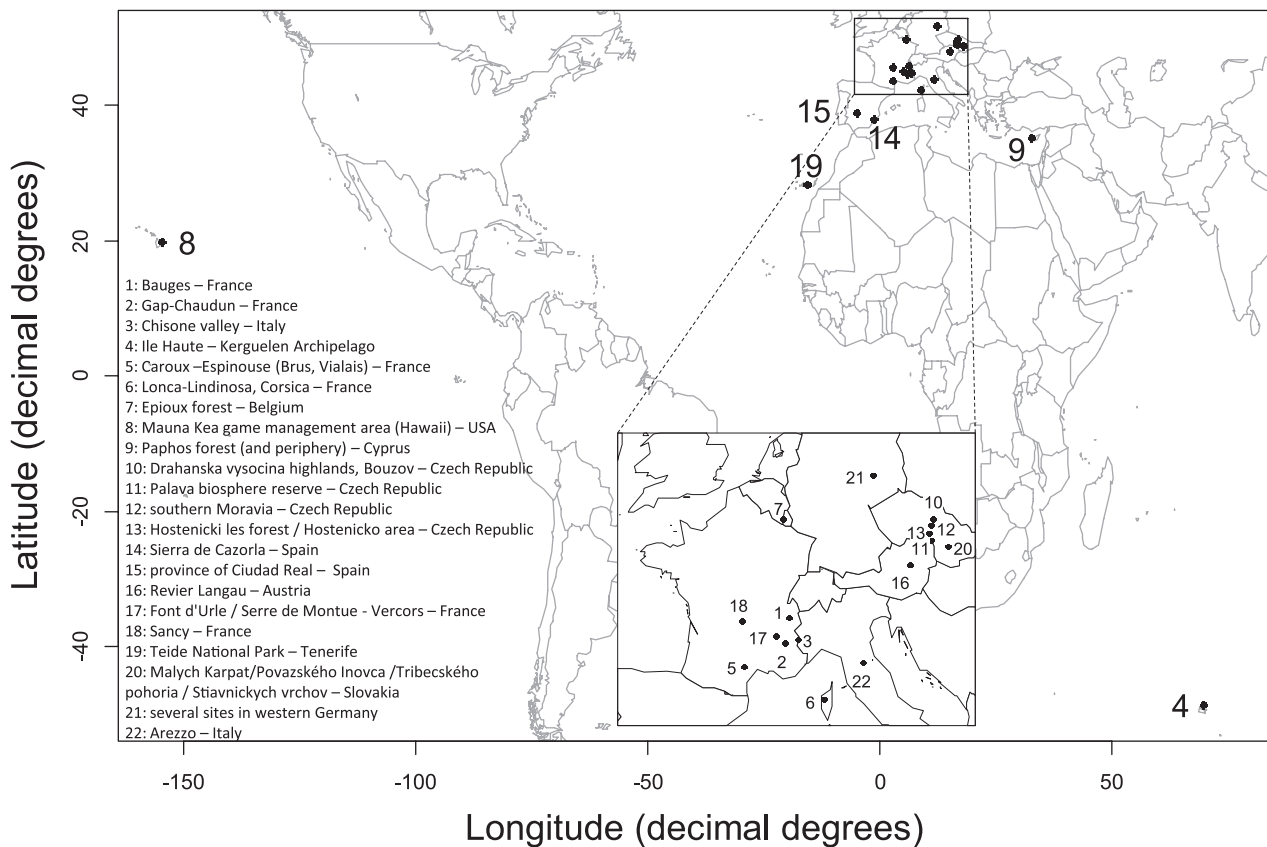


Fig. 1. Locations of the sites (see Table 1) where the diet of mouflon *Ovis gmelini musimon* has been studied (in the 33 studies retained in analysis, resulting in 51 independent data points).

METHODS

Dietary data

We reviewed 42 publications or unpublished reports, each containing data on the diet of mouflon (both Mediterranean island populations *Ovis gmelini musimon* and introduced hybridized populations *Ovis gmelini musimon* × *Ovis* sp.; Table 1 and Appendix S1). We excluded from the analysis of diet variation studies in which the authors used uncommon methods or worked on animals that were not free ranging ($n = 9$, see Appendix S1). Some of the 33 publications we retained (Table 1) included data from more than one study site or season or derived from more than one technique of diet analysis, leading to a total sample size of 51 data points based on rumen content analysis ($n = 30$) and faecal analysis ($n = 21$). Samples were collected from a wide range of habitats in 22 locations, from 155°W to 70°E, 49°S to 51°N and from 0 to 3715 m above sea level (Fig. 1). Results for each food category were expressed as a percentage of the total volume, percentage biomass, percentage of the total number of fragments in samples or a combination

of these percentages (importance index = average of volume- and fragment-based percentages). When the results of studies were expressed in several units, we only included data expressed as percentages of the total number of fragments (the most frequently used measure). Vegetation data were standardized over studies by using seven plant categories, using the definitions of Allen et al. (2011): grasses, forbs, shrubs, seeds and fruits, deciduous trees, coniferous trees and others (see Table 2 and Appendix S2). Each food taxon was assigned to one of these categories following Rameau et al. (1993). When several categories were mixed (e.g. Homolka 1991, mixed shrubs and deciduous trees), we divided equally the value reported into each food category (removing such studies did not change the results qualitatively).

Individual and environmental factors influencing variation in diet

Habitat and season have been reported to be the main determinants of variation in ungulate diets (Kufeld 1973, Kufeld et al. 1973, Tixier & Duncan 1996, Cornelis et al.

Table 1. Summary of the literature on the diet of mouflon reviewed in this study, showing site data, research methods and percentages of each plant category reported in the diet

Authors	Country	Site	Latitude	Longitude	Altitude (m)	Climate	Vegetation	Research technique	Season	n	Grasses	Forbs	Shrubs	Seeds and fruits	Deciduous trees	Coniferous trees	Other
Babad (1997)	France	Bauges	45°40'N	6°13'E	800–2217	Alpine	Mixed closed	Rumen	aw	23	40	16	21		17	5	2
Berulou (unpublished data)	France	Gap-Chaudun	44°38'N	5°59'E	1650–2700	Alpine	Mixed open	Rumen	spsu	18		60	40				
Bertolino et al. (2009)	Italy	Chisone Valley	44°45'N	6°54'E	700–2600	Alpine	Mixed open	Faeces	aw	41		52	45			4	
Chapuis et al. (2001)	Kerqueien Archipelago	Ile Hautet	49°24'S	69°56'E	0–300	Polar	Tundra	Faeces	aw	60	72	24	2		1		
Chauvière (1978)	France	Gap-Chaudun	44°38'N	5°59'E	1650–2700	Alpine	Mixed open	Rumen	aw	30	17	78				6	
Cransac et al. (1997)	France	Caroux-Espinouse (Brs)	43°37'N	2°57'E	600–1098	Mediterranean	Mixed closed	Faeces	spsu	113	33	12	35	3	1	10	15
		Caroux-Espinouse (Vialais)	43°37'N	2°57'E	600–1124	Mediterranean	Mixed closed	Faeces	aw	107	36	4	35	8		3	14
		Lonca – Lindinosat	42°17'N	8°50'E	1400–2200	Mediterranean	Mixed closed	Faeces	spsu	116	37	8	33	4	2	2	15
Deméautis (1981, 1985, 1991)	France							Faeces	aw	105	36	6	37	2	1	4	14
Fallu et al. (1990)	France	Caroux-Espinouse	43°37'N	2°57'E	600–1124	Mediterranean	Mixed closed	Rumen	spsu	7	56	5	4*		3*	3*	30
Fichant (1975)	Belgium	Epioux forest	49°45'N	5°49'E	300–400	Continental	Forest	Rumen	aw	110	10	46	10	15	12	4	4
Griffin (1979)	USA	Mauna Kea Game management area†	19°46'N	155°27'W	2000–3170	Alpine	Mixed closed	Rumen	aw	23	22	1	14	46	14	3	1
		Periphery of Paphos Forest†	35°04'N	32°40'E	400–800	Mediterranean	Mixed closed	Rumen	spsu	56	36	1	11		42	10	5
Hadjisterkotis (1996)	Cyprus							Rumen		1	73	1		11	10		
Heroldova (1988a)	Czech Republic	Paphos Forest†	35°04'N	32°40'E	400–800	Mediterranean	Forest	Rumen	aw	5	91	3	3	4	2		17
		Drahanska vysočina highlands/Bouzov	49°45'N	16°55'E	280–596	Continental	Forest	Rumen	aw	14	39	11	16	11	4	1	
Heroldova (1988b)	Czech Republic	Drahanska vysočina highlands/Bouzov	49°45'N	16°55'E	280–596	Continental	Forest	Rumen	aw	23	10	24	9		35	10	12
Heroldova (1996)	Czech Republic	Palava Biosphere Reserve	48°53'N	16°45'E	151–554	Continental	Mixed closed	Faeces	spsu	60	56	11	30	2			1
Heroldova et al. (2007)	Czech Republic	Drahanska vysočina highlands/Bouzov	49°45'N	16°55'E	280–596	Continental	Forest	Rumen	aw	60	27	10	51	9	33	13	2
		Southern Moravia	49°10'N	16°35'E	100–500	Continental	Mixed open	Rumen	aw	23	19	15	6	5			10
Homolka and Heroldova (1992)	Czech Republic	Hostenický les forest/Hostenicko area	49°30'N	16°47'E	350–500	Continental	Mixed closed	Faeces	aw	6	64	4	6*	1	7*	8*	11
Homolka (1991, 1993)	Czech Republic	Hostenický les forest/Hostenicko area	49°30'N	16°47'E	350–500	Continental	Mixed closed	Faeces	spsu	60	7	38	20*	4	20*	6	6
Maissels (1988)	Cyprus	Paphos Forest†	35°04'N	32°40'E	400–800	Mediterranean	Forest	Faeces	aw	60	8	35	15	12	15	8	7
								Faeces	spsu	54	30	26	33		8	4	
								Faeces	aw	54	37	35	17		9	1	

Martinez and Fandos (1989)	Spain	Sierra de Cazorla	37°57'N	2°50'W	1000–1500	Mediterranean	Mixed open	Rumen	spsu	7	70	14	8*	4*	4*	1
Miranda et al. (2012)	Spain	Province of Ciudad Real	38°55'N	4°16'W	650–820	Mediterranean	Mixed closed	Faeces	aw spsu	8 31	50 22	21 36	12 14*	6 14*	6 14*	4
Onderscheka and Jordan (1974)	Austria	Revier Langau	47°51'N	15°12'E	650–1900	Continental	Forest	Rumen	aw spsu	?	42	31	17	16*	16*	4
Pauthenet (1988)	France	Font d'Urie/Serre de Montlue	44°54'N	5°18'E	600–1706	Alpine	Mixed open	Faeces	aw spsu	?	18	10	8*	5 6*	16	50 1
Redjadj et al. (unpublished data)	France	Bauges	45°40'N	6°13'E	800–2217	Alpine	Mixed closed	Rumen	aw spsu	30 9	42 38	28 33	20 15	7 4	3 8	
Rigaud (1985)	France	Sancy	45°31'N	2°48'E	1000–1886	Alpine	Mixed open	Faeces	aw spsu	90 16	32 45	7 22	18 13	4 11	23 2	11 9
Rodriguez Berrocal and Molera Aparicio (1985)	Spain	Sierra de Cazorla	37°57'N	2°50'W	1000–1500	Mediterranean	Mixed open	Rumen	aw spsu	15 10	33 31*	11 31*	11 7	32 1	7 31*	5 31*
Rodriguez Luengo and Piñero (1991); Rodriguez et al. (1988)	Spain	High Mountain Shrub/riede National Park	28°15'N	16°37'W	1900–3715	Alpine	Mixed closed	Rumen	aw aw	12 14	30* 30*	30* 73	7 27	5	30*	
Sabados and Manica (1977)	Slovakia	Pine Forest/Aricot Malych Karpat/Povazského Inovca/Triebeského pohoria/Štiavnických vrchov	28°09'N	16°30'W	1000–1900	Alpine	Forest	Rumen	aw	11	1	93	6	25	4	5
Stubbe (1971)	Germany	Several sites in western Germany	51°35'N	12°30'E	0–950	Continental	Forest	Rumen	spsu	17	51	38	2	2	9	
Trabalza Marinucci et al. (2005)	Italy	Arezzo	43°49'N	11°43'E	350–1658	Mediterranean	Forest	Rumen	aw spsu	136 4	71 21	8 2	2 25*	2 25*	6 1	4 26

When the same data were used for several publications, only the most detailed results have been used (first cited under 'Authors').
 'aw', autumn and winter; 'spsu', spring and summer; n, number of samples.
 *Data from pooled dietary categories.
 †Island sites.

Table 2. Food categories applied to dietary studies to ensure consistency (see Allen et al. 2011 for detailed definitions). Rameau et al. (1993) was used to assign each taxon to one of these categories (see Appendix S2 for details)

Categories	Description
Grasses	Grasses, sedges (Cyperaceae) and rushes (Juncaceae)
Forbs	Forbs
Shrubs	Shrubs
Seeds and fruits	Seeds and fruits
Deciduous trees	Deciduous trees (buds, leaves, stems and bark)
Coniferous trees	Coniferous trees (buds, needles and bark)
Other	Other (fungi, ferns, lichens, algae and horsetail), unidentified fragments

1999, Gebert & Verheyden-Tixier 2001, Christianson & Creel 2007), so we mainly focused our analysis on these factors. We split data on diet composition by season (spring and summer: period of access to abundant and high-quality food for herbivores; autumn and winter: period of limited access to more sparse and lower-quality food). We described habitat and environmental characteristics at each study site by using four variables (Table 1): habitat types [forests (classified as forest by the authors), mixed closed areas (>50% closed patches), mixed open areas (<50% closed patches) and tundra], broad climate categories (Mediterranean, Continental, Alpine and Polar), altitude [lowlands (<500 m), hills (500–1000 m) and highlands (>1000 m)] and insularity (island and mainland). When studies contained data from several sites, each site was considered as an independent data point, except in studies by Sabados and Manica (1977) and Stubbe (1971), in which results from four neighbouring Slovakian and 11 German sites, respectively, were pooled by the authors. Assuming that variation in habitat characteristics and climatic conditions within each group of sites was less important than variation between the sites investigated in our sample of publications, we chose to include these grouped data as if they were drawn from a single site. Research technique (analysis of faecal samples or samples from the rumen) was expected to affect reported diet composition because being more easily digested, browse is generally less represented in faeces than in rumen contents (and the opposite pattern is observed for grasses; Holechek et al. 1982, Gordon 1995, Cuartas & Garcia-Gonzalez 1996). Apparent variation in diet is expected to occur depending on the way results are expressed (percentage of the total volume, percentage biomass, percentage of the total number of fragments in samples or importance index). Variation is also expected due to gender, age and morphological characteristics (e.g. body mass), but such factors are not accounted for in our review due to the lack of information in dietary studies.

Similarly, effects of site-specific food availability and between-year variation were not assessed. Such information is lacking in most reviews of diet studies due to the coarse resolution (inter-site comparisons) of such approaches (Tixier & Duncan 1996, Gebert & Verheyden-Tixier 2001).

Statistical analyses

The percentage of grass vs. browse consumed is used to classify species on the grazer-browser continuum. As a preliminary step, we therefore plotted the diet content of the three main food items (grasses, forbs and shrubs) according to season, climate, vegetation type, altitude, insularity and the research technique from the studies included in our review. We then analysed separately the diet data array, containing the percentage of each of the seven food items in each data point and the environmental array, containing spatio-temporal environmental characteristics. We used multivariate analyses to identify the main patterns of covariation among diet items and among environmental variables, respectively (see Storms et al. 2008 for a similar approach). We performed principal component analysis on the diet data array, as each variable was expressed as a percentage, and multiple correspondence analysis on the environmental array, where each variable was categorical. Then, we estimated the covariation between the diet data and environmental arrays by performing co-inertia analysis (Dodélec & Chessel 1994, Dray et al. 2003). The overall similarity between the structure of the diet data array and the environmental array was assessed by the co-inertia analysis RV coefficient (multivariate equivalent of R^2 ; Robert & Escoufier 1976), the significance of which was tested by a randomization test (10000 replications; Dray et al. 2003).

RESULTS

In the 42 publications (in Table 1 and Appendix S1 combined), 661 taxa of angiosperms, gymnosperms, ferns, horsetails, fungi, mosses and lichens were reported as consumed by mouflon (Appendix S2). In the 20 publications detailing the identification of food items to a family level, 51 ± 46 (mean \pm standard deviation; range = 14–196) taxa per site were identified. As expected, grasses, forbs and shrubs were, on average, the main sources of food for mouflon and formed 35%, 24% and 16% of the diet over all study sites and seasons, respectively (Table 1). Of the seven diet categories, grasses constituted the highest proportion of the diet in 28 of the 51 data points; forbs were the highest in 13 and shrubs in six data points (Table 1). All environmental variables were found to explain part of the variation in the content of these three food items (Fig. 2).

Most of the observed variation in the diet data array was accounted for by the three first axes (25%, 21% and 17%,

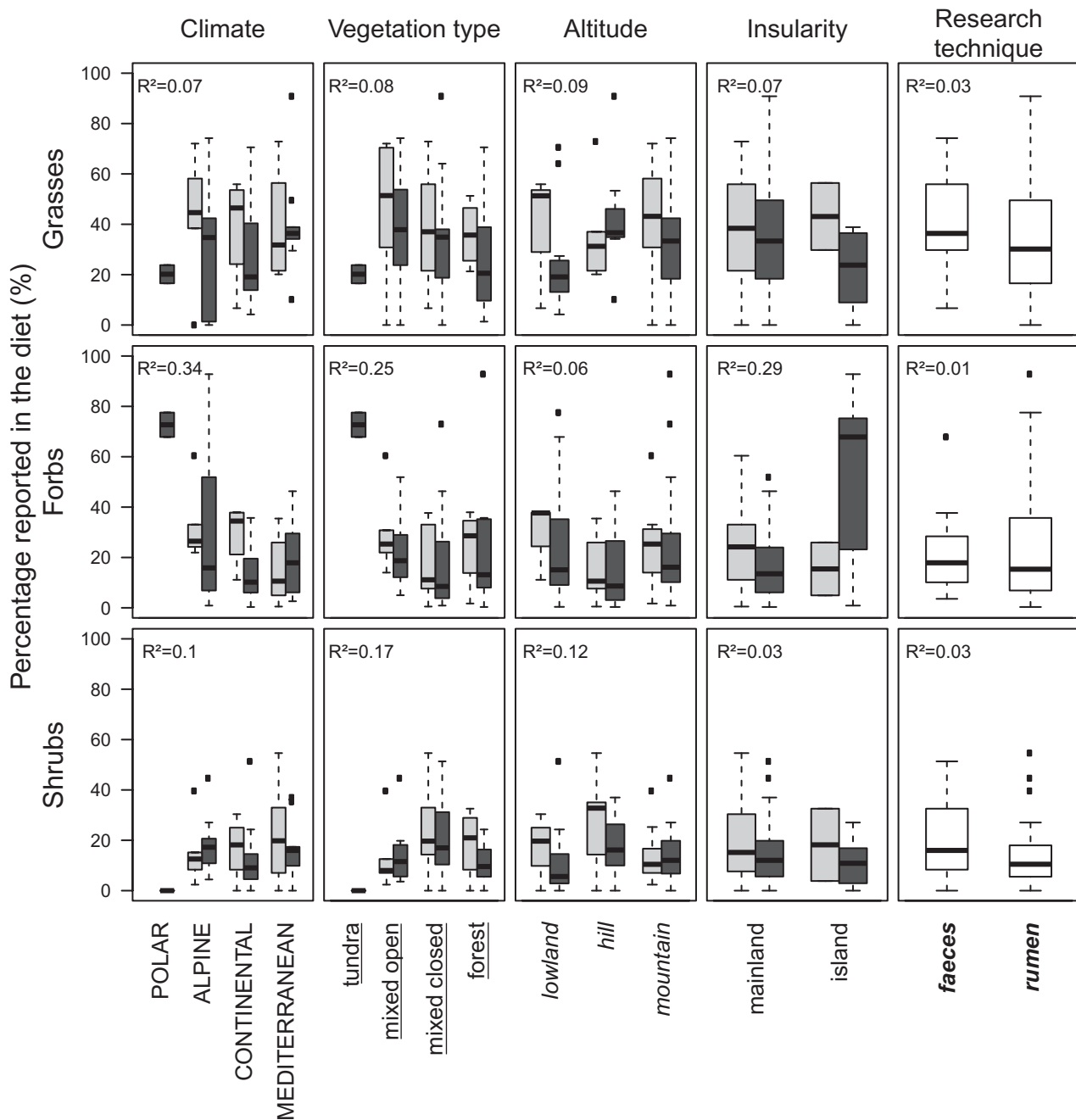


Fig. 2. Variation in documented mouflon *Ovis gmelini musimon* diet (% of grasses, forbs and shrubs) according to the main environmental factors (seasons, climate, vegetation types, altitude and insularity) and research techniques, recorded from 51 reviewed data points on the diet of mouflon. The proportion of variation explained by each factor for each botanical entity (R^2) is given in the top left corner of each graph. Data from the spring and summer are in light grey; those from autumn and winter are in dark grey. Climate types are labelled in capital letters. Vegetation (underlined) was categorized as tundra (Kerguelen Archipelago), mixed open (<50% closed areas), mixed closed (>50% closed areas) and forest (classified as forest by the authors). Altitude ranges (in italics) were lowlands (<500 m), hills (500–1000 m) and mountains (>1000 m). Research techniques are labelled in bold italic. For each group, horizontal lines (low, thick line and high) represent first, median and third quartile of the distributions, respectively. Dashed lines show either the maximum value or 1.5 times (roughly two standard deviations) the interquartile range (i.e. the difference in the response variable between its first and third quartiles) of the data. Points more than 1.5 times the interquartile range (above the third quartile or below the first quartile) are plotted individually.

respectively; total of 63%) of the principal component analysis. The first axis contrasted forbs and shrubs with grasses and trees (Fig. 3a and b). The second axis opposed grasses to trees, and seeds and fruits. The third axis opposed diets containing seeds and fruits to those containing the 'other' category.

Most of the observed variation in the environmental data array was accounted for by the three first axes (24%, 19% and 18%, respectively; total of 61%) of the multiple correspondence analysis. The first axis distinguished the Kerguelen Archipelago, southern Indian Ocean (the only polar study site) from the other sites (Fig. 3c and d). The second axis opposed data from mixed open mountainous areas to data from hilly mixed closed Mediterranean ones. While confirming the particularity of the Kerguelen Archipelago, the third axis also distinguished data from continental forests.

Most of the co-structure between the diet data array and the environmental array (86%) was explained by the two first axes of the co-inertia analysis, which accounted for 52% and 34% of this co-structure, respectively (Fig. 4). The co-inertia analysis RV coefficient was 0.20, significantly greater than the value obtained from 10000 random permutations of the rows of the two tables (0.12; $P = 0.005$).

The first axis of the co-inertia analysis highlighted the specificity of mouflon diets in two sites (represented by four data points): the Kerguelen Archipelago and Teide National Park, Canary Islands, Spain. Diets in these sites had high positive values on axis 1, i.e. high proportions of forbs (Fig. 4).

The plot of the two first axes structured the data according to broad climatic or vegetation features (Fig. 4a). Data from continental forests situated at low altitudes, characterized by negative values on axis 2, were opposed to the data from other sites, which had positive values on axis 2. However, data from hilly mixed closed sites with Mediterranean mild conditions, characterized by negative values on axis 1, contrasted with data from mountainous mixed open areas, which displayed positive values on axis 1. Diets from continental areas were characterized by high proportions of seeds, fruits and trees and lower proportions of shrubs and grasses. Diets from Mediterranean areas were characterized by higher proportions of shrubs and grasses, whereas higher proportions of forbs were found in diets from mountainous sites. The second axis also corresponded to a season \times research technique gradient. Spring and summer diets and/or diets described from faecal samples contained higher proportions of grasses and shrubs, whereas autumn and winter diets and/or those described from rumen samples were characterized by higher proportions of seeds and fruits, coniferous and deciduous trees.

Results from the co-inertia analysis were grouped according to habitat \times season and habitat \times research technique variations (Fig. 5). Sites were reclassified into five

groups based on their position on the two first axes of the co-inertia analysis: (i) areas with Mediterranean climate; (ii) areas with alpine climate; (iii) areas with continental climate; (iv) Kerguelen Archipelago; and (v) Teide National Park. Seasonal variation was found to be particularly important at sites with alpine and continental climates (Fig. 5a and Table 3). Mouflon shifted from a grass- and forb-rich diet during spring and summer (76% of food intake at sites with alpine climate, 68% at sites with continental climate) to a diet containing higher proportions of seeds, fruits and trees during autumn and winter (21% at sites with alpine climate and 33% at sites with continental climate). In Mediterranean areas, seasonal variation appeared to be more limited: the diet contained more shrubs during spring and summer (higher values on axis 2) and more seeds, fruits and trees during autumn and winter (lower values on axis 2). Both Fig. 5a and Table 3 revealed that mouflon diet on the Kerguelen Archipelago and at the Teide National Park was unusual as forbs constituted the major component of autumn and winter diets at both sites (>72% on the Kerguelen Archipelago and >81% in the Teide National Park).

Comparing results derived from faecal samples with those from rumen content samples showed slight differences in the four habitat types where it was possible to consider such analyses (Fig. 5b). In the Kerguelen Archipelago, Mediterranean, mountain and continental areas, data from faecal samples displayed higher values than data from rumen samples on the second axis, suggesting that higher proportions of grasses and shrubs, and lower proportions of seeds, fruits and trees were obtained from faeces than from rumen contents.

DISCUSSION

Common patterns in diet composition

Our comparative analyses allowed us to identify common patterns and to evaluate the extent and causes of intraspecific variability in the diet of mouflon. As already documented, this species included a large proportion of grass in its diet (García-González & Cuartas 1989, Faliu et al. 1990, Homolka 1993, Cransac et al. 1997, Heroldova et al. 2007, Bertolino et al. 2009, Redjadj 2010). However, mouflon fed on a very wide range of plant species (see Appendix S2). At several sites in the Czech Republic, Mottl (1960) found up to 196 species in the diet of mouflon and Pfeffer (1967) published a list of 95 taxa consumed in Corsica. However, this dietary diversity reflects the huge diversity of habitats in which mouflon are found (Fig. 1). Indeed, at the intra-site level, data suggest that the breadth of mouflon diet is similar to that of sympatric herbivore species. In the Czech Republic, the average numbers of plant species consumed

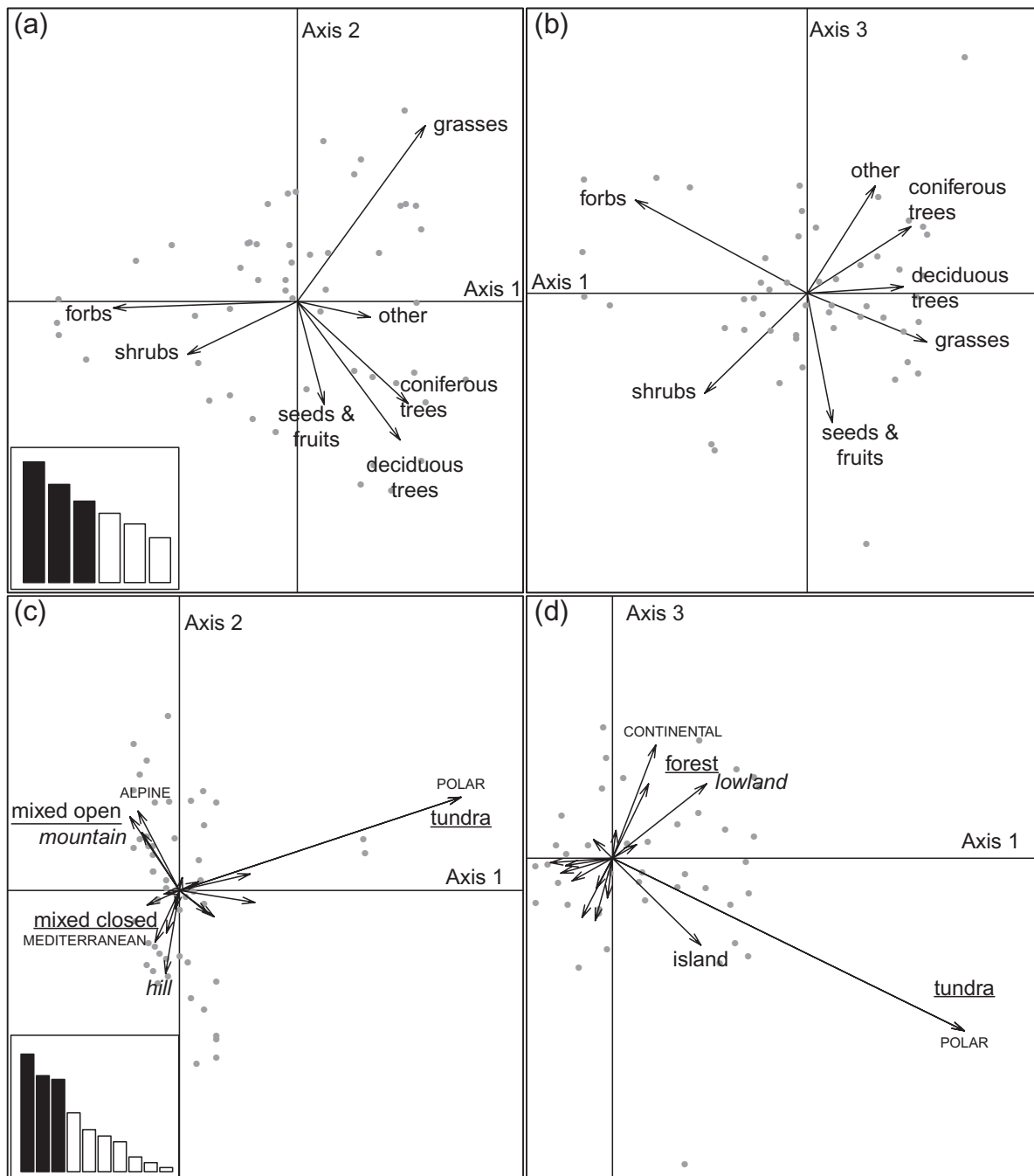


Fig. 3. Projection of the diet of mouflon *Ovis gmelini musimon* from each data point (publication × site × season × technique; grey dots) against food items (arrows) on the first (horizontal) and second (vertical; a) and on the first (horizontal) and third (vertical; b) axes of the principal component analysis [representation of the proportion of diet variation explained by each of the six axes is given in the bottom left corner of (a)]. Food items were categorized according to Table 2. Projection of the diet of mouflon from each data point (publication × site × season × technique; grey dots) against environmental variables (arrows) on the first (horizontal) and second (vertical; c) and on the first (horizontal) and third (vertical; d) axes of the multiple correspondence analysis [representation of the proportion of environmental variation explained by each axis is given in the bottom left corner of (c)]. For clarity, only the arrows representing environmental variables allowing axes interpretation are labelled. Vegetation (underlined) was categorized as tundra (Kerguelen Archipelago), mixed open (<50% of closed areas), mixed closed (>50% of closed areas) and forest (classified as forest by the authors). Climate types (in capitals) were categorized as continental, alpine, Mediterranean or polar. Altitude ranges (in italics) were lowlands (<500 m), hills (500–1000 m) and mountains (>1000 m). Islands were also distinguished (as island or mainland). Season opposed spring and summer to autumn and winter. Diets were analysed using faeces or rumen contents.

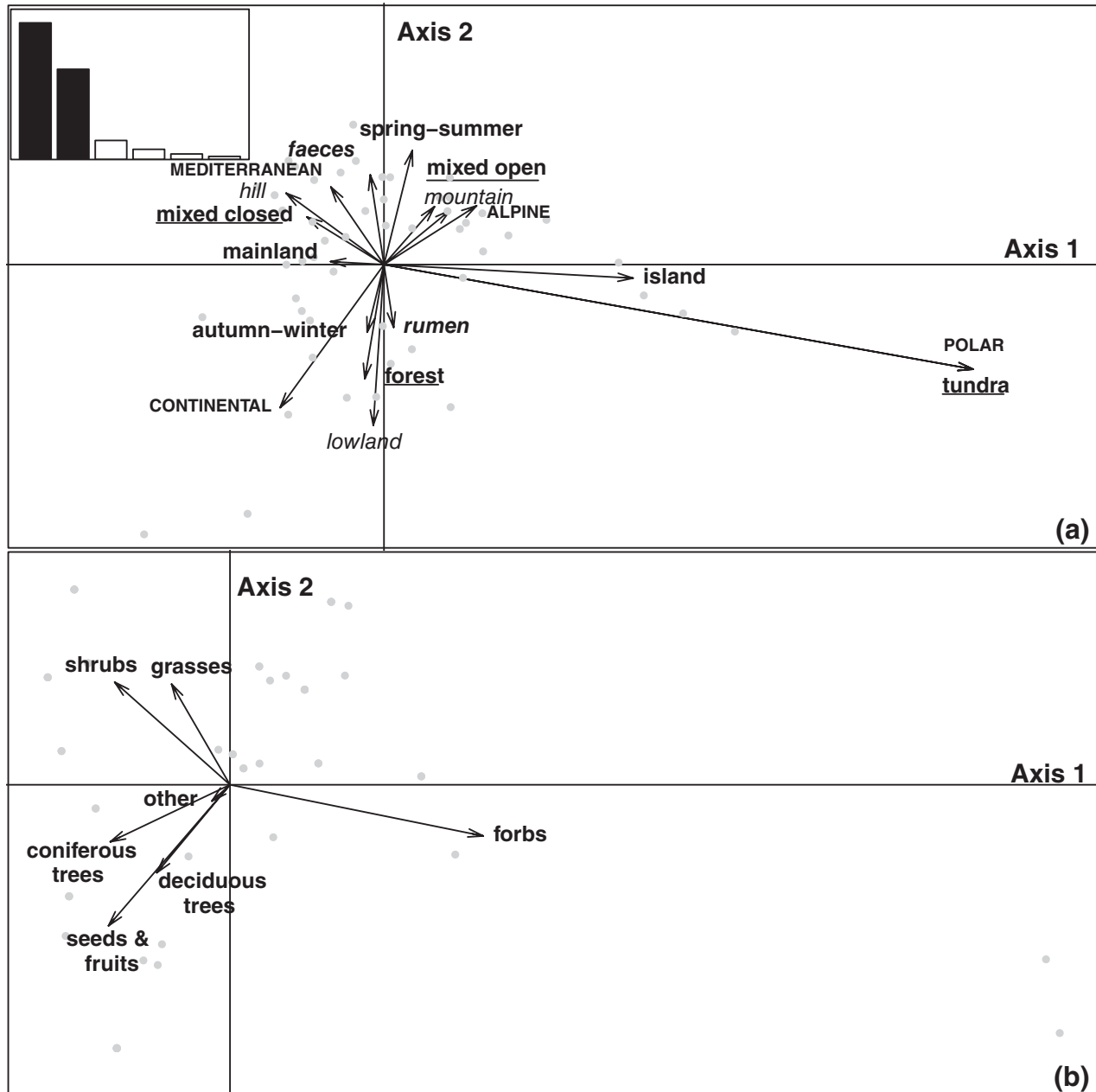


Fig. 4. Projection of (a) the diet of mouflon *Ovis gmelini musimon* from each data point (publication × site × season × technique; grey dots) against environmental variables (arrows) and (b) against food items on the first (horizontal) and second (vertical) co-inertia axes (representation of the proportion of co-inertia explained by each of the six axes is given in the top left corner). Food items were categorized according to Table 2. Vegetation (underlined) was categorized as tundra (Kerguelen Archipelago), mixed open (<50% of closed areas), mixed closed (>50% of closed areas) and forest (classified as forest by the authors). Climate (in capitals) was categorized as continental, mountain, Mediterranean or polar. Altitude ranges (in italics) were lowlands (<500 m), hills (500–1000 m) and mountains (>1000 m). Islands were also distinguished (as island or mainland). Season (in bold) opposed spring and summer to autumn and winter. Diets were analysed using faeces or rumen contents, and research techniques are shown in bold italics.

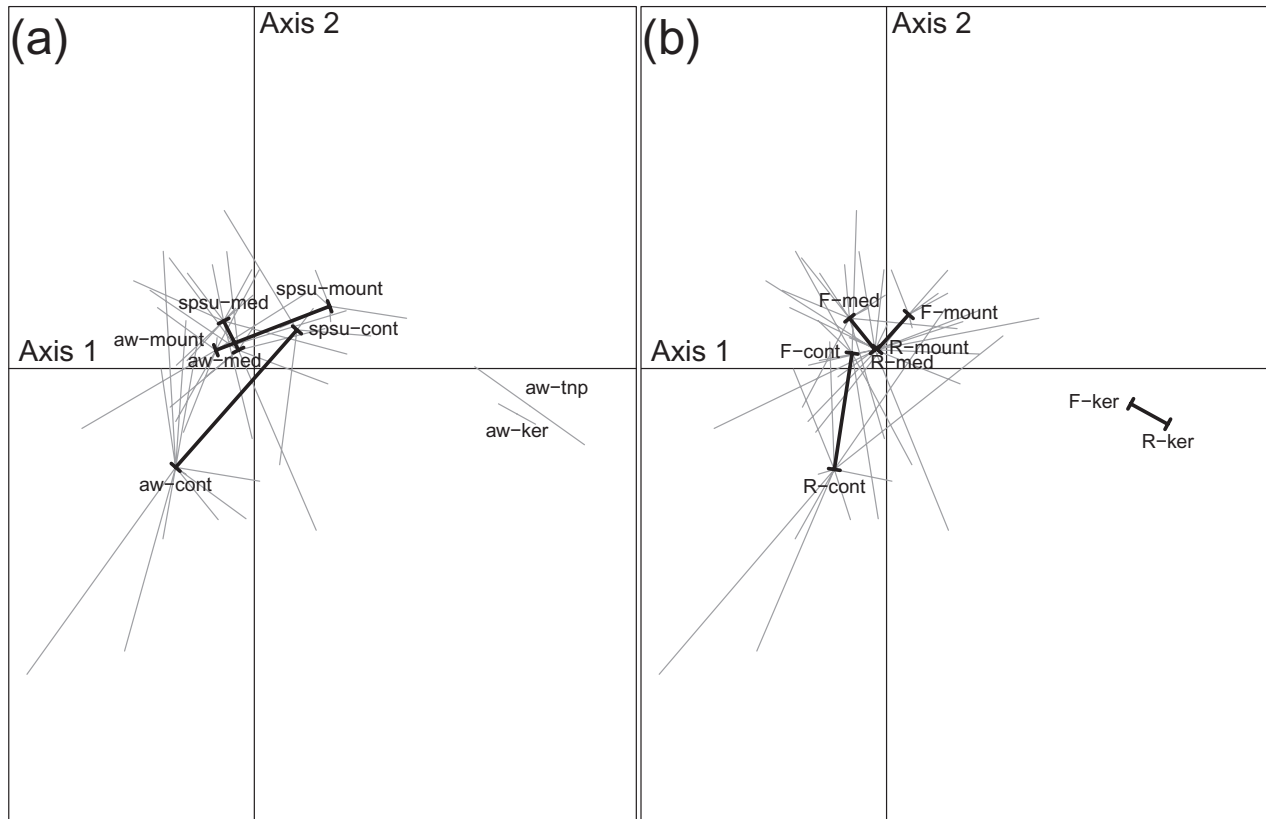


Fig. 5. Projection of the diet of mouflon *Ovis gmelini musimon* according to habitat types (see the text for details) and (a) seasons and (b) research techniques. ‘med’, Mediterranean; ‘cont’, Continental; ‘mont’, Mountain; ‘ker’, Kerguelen Archipelago, ‘tnp’, Teide National Park; ‘spsu’, spring–summer; aw, autumn–winter; ‘F’, faeces; ‘R’, rumen. Grey lines relate points for a given habitat type and season (a) or research technique (b) to their gravity centre. The shifts in gravity centre from spring–summer to autumn–winter (a) and from faeces to rumen (b) are indicated where possible by black lines for each habitat type.

annually by sympatric populations of roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, wild goat *Capra aegagrus* and mouflon were 47–49, 45, 56 and 48–52, respectively (Homolka 1993, Heroldova 1996). In the French Alps,

Redjadj (2010) identified 109 species for roe deer, 151 for chamois *Rupicapra rupicapra*, 136 for red deer and 141 for mouflon in faeces collected from September to January.

Table 3. Average percentages of the dietary components found in mouflon rumen content and faeces in the main habitat types highlighted by the co-inertia analysis and seasons

Habitat type	Seasons	<i>n</i>	Grasses	Forbs	Shrubs	Seeds and fruits	Deciduous trees	Coniferous trees	Other
Mediterranean	spsu	10	39	14	21	3	7	3	12
	aw	9	40	19	17	5	6	4	9
Continental	spsu	4	39	30	17	1	6	3	5
	aw	11	29	14	13	11	16	7	11
Mountainous	spsu	5	43	33	16	0	4	1	4
	aw	8	40	17	18	1	13	7	5
Teide National Park	aw	2	1	83	17	0	0	0	0
Kerguelen Archipelago	aw	2	20	73	0	0	0	0	7

The sources are listed in Table 1.

‘aw’, autumn and winter; ‘spsu’, spring and summer; *n*, number of data points (as defined in the text).

Variation in diet

Our review highlighted the strong specificity of mouflon diets in the Kerguelen Archipelago (Chapuis et al. 2001) and the Teide National Park (Rodríguez Luengo & Piñero 1991). Populations inhabiting these sites showed unusual feeding strategies: forbs made up more than 70% of food intake, while very low proportions of grass and grass-like species (i.e. sedge and rush species, see Allen et al. 2011) were eaten, and shrubs and trees were eaten in very small quantities or not at all. These sites represent extreme cases where harsh local environmental conditions result in poor vegetation diversity and a lack of grasses (see Rodríguez Luengo & Piñero 1991, Leuschner 1996, Santin-Janin et al. 2009 for descriptions of the vegetation of each site). Trees are also absent in the Kerguelen Archipelago.

Seasonal variation in growth and related accessibility and palatability of vegetation (Langvatn et al. 1996) influenced mouflon diet composition. In highly seasonal environments such as mountains and the continental forests of central Europe, mouflon consumed high proportions of grass and grass-like species during spring and summer, when these items were available and at their most palatable. During autumn and winter, they shifted towards seeds, fruits and trees, when preferred food was less available (e.g. because of snow cover) and/or of lower quality or digestibility. In Mediterranean areas, seasonal diet variation was less marked than in other habitats. Diet composition is thus strongly influenced by environmental seasonality.

Similar studies reviewing data on the diet of large herbivores and causes of variation are available (e.g. Tixier & Duncan 1996, Cornelis et al. 1999 for European roe deer; Kufeld 1973 for Rocky Mountain populations of elk *Cervus canadensis*; Christianson & Creel 2007 for western North American populations of elk; Gebert & Verheyden-Tixier 2001 for European red deer; Kufeld et al. 1973 for Rocky Mountain mule deer *Odocoileus hemionus*; Peek 1974, Schwartz 1992 for North American moose *Alces alces*; and Todd 1972 for bighorn sheep *Ovis canadensis*). When investigated, variation in diet due to habitat and season was always revealed, highlighting the major influence of both factors on feeding ecology of large herbivore species.

The techniques used to investigate mouflon diet probably explained some of the variation found. Higher proportions of seeds, fruits and trees were found in results derived from samples of rumen contents than in those derived from faecal samples, which were characterized by large proportions of grasses and shrubs. The differential digestibility of plant epidermis during passage through the digestive tract could result in such a pattern (Vavra et al. 1978, McInnis et al. 1983): browse is underrepresented in faeces because it is more digestible than grass. Variation due to research techniques could not be separated from seasonal variation

because rumens were mostly available during hunting periods (i.e. autumn and winter); both season and technique influenced reported mouflon diet. This probably explained the large range of variation observed in Fig. 5a and b in continental areas compared with other habitats. In continental areas, autumn and winter diets were mostly (in eight out of 11 data points) investigated from rumen contents, while faeces were preferred in spring and summer (three out of five data points). However, such a bias was not observed in other habitats, so we are confident that both seasonality and research techniques influenced mouflon diet as reported by researchers. In other reviews of the diets of large herbivores, the influence of research techniques on reported diet composition was only noted by Cornelis et al. (1999) while Christianson and Creel (2007) found no significant effect of this factor. Future studies should rely on new developing technologies, such as DNA barcoding (Valentini et al. 2009a, b) to try to overcome the confounding effect of research techniques in diet studies.

Are mouflon really grazers?

Several adaptations considered typical of 'cattle-type' ruminants (which mostly feed as grazers) have been attributed to the mouflon in comparative analyses of ruminant morphophysiology (for a complete list, see Clauss et al. 2009b). For instance, compared with a species largely recognized as a browser (roe deer; Tixier & Duncan 1996), mouflon possess a larger reticulo-rumen (Dreschner-Kaden 1976) characterized by a peculiar mucosal membrane (Kamler 2001, Clauss et al. 2009b). Rumen content is less viscous and more stratified than in the roe deer (Clauss et al. 2009b), allowing a longer retention time (Behrend et al. 2004) and hence optimal use of low-quality vegetation. However, despite these morphophysiological characteristics, our data showed that mouflon diet may include high proportions of forbs, shrubs and/or trees (Table 3) and is close to the assemblage expected for mixed or intermediate feeders (such as red deer, Alpine ibex *Capra ibex*, chamois and European bison *Bison bonasus*; Van Wieren 1996, Gebert & Verheyden-Tixier 2001). Furthermore, in most studies we reviewed, thresholds of >75% (Pérez-Barbería & Gordon 1999, Pérez-Barbería et al. 2001b, Mendoza et al. 2002) or >90% (Janis 1990, Pérez-Barbería et al. 2001a) of grass in the diet, commonly used to define grazers, were not reached. Therefore, the mouflon cannot be considered to be an obligate grazer but rather is a variable grazer (*sensu* Gagnon & Chew 2000 and Codron et al. 2007), i.e. a species that 'consumes low but significant amounts of dicots', even though thresholds set by Gagnon and Chew (2000) are higher (60–90% of grass) than observed in our review (0–91%; Table 1). The same conclusion was reached by Todd (1972), who suggested, in a review of the diet of bighorn sheep, that not only the importance of grasses but

also the ability to cope with forbs, shrubs and tree foliage in some situations could be shared by other wild ovines, as is generally observed for 'cattle-type' ruminants (Van Wieren 1996, Clauss et al. 2003). These results provided additional support to Pérez-Barbería et al. (2004) and Codron and Clauss (2010) who suggested that species should be classified by two characteristics: the average proportion of grasses eaten, and the range of grass content in the diet, both of which are probably constrained by ecological factors and digestive morphophysiology.

Regarding ecological factors, the propensity of mouflon to browse may be linked with their introduction into novel and distinct areas. This observation could be interpreted as evidence of a mismatch between the digestive features of mouflon and their diets in the range of habitats where they can be found. Indirect support for the existence of such a mismatch was found in a population facing habitat loss (in Caroux-Espinouse, France, see Table 1), for which decreasing open ranges by up to 50% in 37 years contributed to a long-term decrease in body mass (Garel et al. 2007). The fact that mouflon have been able to maintain populations in a large range of habitats, even where grasses are very uncommon or unavailable, raises questions, on the one hand, about the extent to which 'cattle-type' species are able to include plants other than grasses in their diet (Clauss et al. 2010, Codron & Clauss 2010) and, on the other hand, about the long-term persistence of most of these populations. Detailed studies of digestive morphophysiology of mouflon, analysis of the success or failure of past introductions, and comparative analyses of population dynamics and the proportion of grasses in the diets within this range of habitats should allow these questions to be answered.

Implications for management and conservation

Several native (e.g. Anatolian mouflon; Özütl 2009) and feral populations (Vigne 1992) of mouflon on Mediterranean islands are of conservation concern (Cassola 1985, Shackleton & IUCN/SSC Caprinae Specialist Group 1997, Hadjisterkotis 2001). In contrast, the success of the introduction of mouflon as a game species all over the world has allowed the development of thriving businesses based on trophy hunting (Shackleton & IUCN/SSC Caprinae Specialist Group 1997, Hofer 2002). Income from hunting can be used to fund habitat improvement for mouflon, e.g. clear cutting and range burning, which are known to be effective (Cazau et al. 2011) and may thereby counteract the phenotypic and economic consequences of habitat modification (Garel et al. 2007). Furthermore, creating attractive areas for introduced populations of mouflon in specific locations could limit competition with native ungulate species (Bertolino et al. 2009), damage to commercial forests (often

important local sources of income) and impacts on local biodiversity (Chapuis et al. 1994, Garzón-Machado et al. 2012). In this paradoxical context of managing rarity (native and island Mediterranean populations), as well as quality and abundance (introduced and harvested populations), our review should help managers by providing information on mouflon diet and on the range of habitats in which mouflon are able to persist, thus enhancing our understanding of the place of mouflon in ecosystems, especially where they were introduced and may compete with a guild of native ungulates (Bertolino et al. 2009, Redjadj 2010). Assessing the carrying capacity of habitats and predicting short- to long-term changes in habitats are both essential requirements to ensure the conservation and persistence of healthy mouflon populations and locally important economic activities related to them (Gordon et al. 2004) in the context of the expansion of ungulates throughout Europe (Loison et al. 2003) and changes in land use and climate (Acevedo et al. 2011, Mysterud & Sæther 2011). Finally, information on feeding niches and their breadth is essential to interpret the increasing numbers of studies of habitat selection and ecological niche that are being facilitated by global positioning system technology (Cagnacci et al. 2010). In the near future, a challenge for ecologists will be to collect data on variation in fitness components in relation to habitat characteristics in order to identify 'key resources' (*sensu* Illius & O'Connor 2000), i.e. resources on which individual survival, reproduction and hence population dynamics and persistence may depend (Gaillard et al. 2010).

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REFERENCES

- Acevedo P, Farfán MA, Márquez AL, Delibes-Mateos M, Real R, Vargas JM (2011) Past, present and future of wild ungulates in relation to changes in land use. *Landscape Ecology* 26: 19–31.
- Allen VG, Batello C, Berretta EJ, Hodgson J, Kothmann M, Li X et al. (2011) An international terminology for grazing lands and grazing animals. *Grass and Forage Science* 66: 2–28.
- Babad G (1997) *Etude des Relations entre un Peuplement Animal et la Végétation : Impacts du Chamois, du Chevreuil et du Mouflon sur les Peuplements Forestiers dans la Réserve Nationale de Faune Sauvage et de Chasse des Bauges (Savoie)*. PhD thesis, Université de Savoie, France.

- Behrend A, Lechner-Doll M, Streich WJ, Clauss M (2004) Seasonal faecal excretion, gut fill, liquid and particle marker retention in mouflon *Ovis ammon musimon*, and a comparison with roe deer *Capreolus capreolus*. *Acta Theriologica* 49: 503–515.
- 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.
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365: 2157–2162.
- Cassola F (1985) Management and conservation of the Sardinian mouflon (*Ovis musimon* Schreber): an outline. In: Lovari S (ed.) *The Biology and Management of Mountain Ungulates*, 197–203. Croom Helm, London, UK.
- Cazau M, Garel M, Maillard D (2011) Responses of heather moorland and Mediterranean mouflon foraging to prescribed-burning and cutting. *The Journal of Wildlife Management* 75: 967–972.
- Chapuis JL, Boussès P, Barnaud G (1994) Alien mammals, impact and management in the French subantarctic islands. *Biological Conservation* 67: 97–104.
- Chapuis JL, Boussès P, Pisanu B, Réale D (2001) Comparative rumen and fecal diet microhistological determinations of European mouflon. *Journal of Range Management* 54: 239–242.
- Chauvière M (1978) *Le Mouflon de Corse (Ovis ammon musimon) – Etude de la Population Implantée dans le Massif de Chaudun (Hautes-Alpes)*. Technical report, Ecole Nationale des Ingénieurs des Travaux des Eaux et Forêts, Nogent-sur-Vernisson, France.
- Christianson DA, Creel S (2007) A review of environmental factors affecting elk winter diets. *The Journal of Wildlife Management* 71: 164–176.
- Clauss M, Lechner-Doll M, Streich WJ (2003) Ruminant diversification as an adaptation to the physicochemical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos* 102: 253–262.
- Clauss M, Fritz J, Bayer D, Hummel J, Streich WJ, Südekum KH, Hatt JM (2009a) Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*). *Zoology* 112: 195–205.
- Clauss M, Hofmann RR, Fickel J, Streich WJ, Hummel J (2009b) The intraruminal papillal gradient in wild ruminants of different feeding types: implications for rumen physiology. *Journal of Morphology* 270: 929–942.
- Clauss M, Hume ID, Hummel J (2010) Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal* 4: 979–992.
- Codron D, Clauss M (2010) Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. *Canadian Journal of Zoology* 88: 1129–1138.
- Codron D, Codron J, Lee-Thorp JA, Sponheimer M, De Ruiter D, Sealy J, Grant R, Fourie N (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology* 273: 21–29.
- Cornelis J, Casær J, Hermy M (1999) Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): a review. *Journal of Zoology* 248: 195–207.
- Cransac N, Valet G, Cugnasse JM, Rech J (1997) Seasonal diet of mouflon (*Ovis gmelini*): comparison of population sub-units and sex-age classes. *Revue d'Ecologie* 52: 21–36.
- Cuartas P, Garcia-Gonzalez R (1996) Review of available techniques for determining the diet of large herbivores from their faeces. *Oecologia Montana* 5: 47–50.
- Cugnasse JM (1994) Révision taxinomique des mouflons des îles méditerranéennes. *Mammalia* 58: 507–512.
- Deméautis G (1981) *Rapport d'étude sur le Mouflon de Corse*. Technical report, Parc Naturel Régional de Corse, Corsica, France.
- Deméautis G (1985) Eco-épidémiologie parasitaire – éléments d'enquête autour d'un ongulé sauvage corse, le mouflon (*Ovis ammon musimon* Schreber, 1782). *Bulletin d'Information sur les Pathologies des Animaux Sauvages* 3: 65–82.
- Deméautis G (1991) *Le Régime Alimentaire du Mouflon de Corse: Bases Bibliographiques Générales et Méthodologiques Vétérinaires et Éco-éthologiques de Son Étude*. PhD thesis, Ecole Nationale Vétérinaire, Toulouse, France.
- Dodélec S, Chessel D (1994) Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology* 31: 277–294.
- Dray S, Chessel D, Thioulouse J (2003) Co-inertia analysis and the linking of ecological data tables. *Ecology* 84: 3078–3089.
- Dreschner-Kaden U (1976) Untersuchungen am Verdauungstrakt von Reh, Damhirsch und Mufflon Mitteilung 1: Gewichtserhebungen und Kapazitätmessungen am Verdauungstrakt, insbesondere am Pansen-Haubenraum von Reh, Damhirsch und Mufflon. *Zeitschrift für Jagdwissenschaften* 22: 184–190.
- Duncan A, Poppi D (2008) Nutritional ecology of grazing and browsing ruminants. In: Gordon IJ, Prins HHT (eds) *The Ecology of Browsing and Grazing*, 89–116. Springer Verlag, Berlin, Heidelberg, Germany.
- Faliu L, Cugnasse JM, Auvray F, Orliac D, Rech J (1990) Le régime alimentaire du mouflon de Corse (*Ovis ammon musimon*) dans le massif du Caroux-Espinouse d'après l'analyse du contenu de 125 panses. *Revue de Médecine Vétérinaire* 141: 545–556.
- Fichant R (1975) Introduction d'une espèce allochtone, le mouflon (*Ovis musimon* Pallas) dans la forêt de la Basse-Semois et détermination de son alimentation en période automnale. *Royal Saint-Hubert Club de Belgique* 4: 135–138.

- Gagnon M, Chew A (2000) Dietary preferences in extant African Bovidae. *Journal of Mammalogy* 81: 490–511.
- Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B (2010) Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365: 2255–2265.
- García-González R, Cuartas P (1989) A comparison of the diets of the wild goat (*Capra pyrenaica*), domestic goat (*Capra hircus*), mouflon (*Ovis musimon*), and domestic sheep (*Ovis aries*) in the Cazorla mountain range. *Acta Biologica Montana* 9: 123–132.
- Garel M, Cugnasse JM, Maillard D, Gaillard JM, Hewison AJM, Dubray D (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications* 17: 1607–1618.
- Garzón-Machado V, González-Mancebo JM, Palomares-Martínez A, Acevedo-Rodríguez A, Fernández-Palacios JM, Del-Arco-Aguilar M, Pérez-de-Paz PL (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biological Conservation* 143: 2685–2694.
- Garzón-Machado V, del Arco-Aguilar MJ, Pérez-de Paz PL (2012) Threat or threatened species? A paradox in conservation biology. *Journal for Nature Conservation* 20: 228–230.
- Gebert C, Verheyden-Tixier H (2001) Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. *Mammal Review* 31: 189–201.
- Geiger G, Hofmann RR, König R (1977) Vergleichend-anatomische Untersuchungen an den Vormägen von Damwild (*Cervus dama*) und Muffelwild (*Ovis ammon musimon*). *Säugetierkundliche Mitteilungen* 25: 7–21.
- Giffin JG (1979) *Ecology of the Mouflon Sheep on Mauna Kea*. Pittman-Robertson project No. W-17-R, Study no. R-III 1975-1979. Technical report, State of Hawaii – Department of Land and Natural Resources – Division of Forestry and Wildlife, USA.
- Gordon IJ (1995) Animal-based techniques for grazing ecology research. *Small Ruminant Research* 16: 203–214.
- Gordon IJ, Hester AJ, Festa-Bianchet M (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41: 1021–1031.
- Hadjisterkotis E (1996) Ernährungsgewohnheiten des Zyprischen Mufflons *Ovis gmelini ophion*. *Zeitschrift für Jagdwissenschaft* 42: 256–263.
- Hadjisterkotis E (2001) The Cyprus mouflon, a threatened species in a biodiversity 'hotspot' area. In: Nahlik A, Uloth W (eds) *Proceedings of the Third International Symposium on Mouflon*, 71–81. Institute of Wildlife Management, Sopron, Hungary.
- Heroldova M (1988a) The diet of mouflon (*Ovis musimon*) outside the growing period 1983–1984. *Folia Zoologica* 37: 309–318.
- Heroldova M (1988b) Method of mouflon (*Ovis musimon*) diet research. *Folia Zoologica* 37: 113–120.
- Heroldova M (1996) Dietary overlap of three ungulate species in the Palava Biosphere Reserve. *Forest Ecology and Management* 88: 139–142.
- Heroldova M, Homolka M, Kamler J, Koubek P, Forejtek P (2007) Foraging strategy of mouflon during the hunting season as related to food supply. *Acta Veterinaria Brno* 76: 195–202.
- Hofer D (2002) *The Lion's Share of the Hunt: Trophy Hunting and Conservation: A Review of the Legal Eurasian Tourist Hunting Market and Trophy Trade Under CITES*. Technical report, TRAFFIC Europe, Brussels, Belgium.
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443–457.
- Holeček JL, Vavra M, Pieper RD (1982) Botanical composition determination of range herbivore diets: a review. *Journal of Range Management* 3: 309–315.
- Homolka M (1991) The diet of mouflon (*Ovis musimon*) in the mixed forest habitat of the Drahanská vrchovina highland. *Folia Zoologica* 40: 193–201.
- Homolka M (1993) The food niches of three ungulate species in a woodland complex. *Folia Zoologica* 42: 193–203.
- Homolka M, Heroldova M (1992) Similarity of the results of stomach and faecal contents analyses in studies of the ungulate diet. *Folia Zoologica* 41: 193–208.
- Illius AW, O'Connor TG (2000) Resource heterogeneity and ungulate population dynamics. *Oikos* 89: 283–294.
- Janis CM (1990) Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodoids and ungulates. *Memoirs of the Queensland Museum* 28: 349–366.
- Kamler J (2001) Morphological variability of forestomach mucosal membrane in red deer, fallow deer, roe deer and mouflon. *Small Ruminant Research* 41: 101–107.
- Kufeld RC (1973) Foods eaten by the Rocky Mountain elk. *Journal of Range Management* 26: 106–113.
- Kufeld RC, Wallmo OC, Feddema C (1973) *Foods of the Rocky Mountain Mule Deer*. Technical Report USDA Forest Service Research Paper RM-111, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* 65: 653–670.
- Leuschner C (1996) Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. *Plant Ecology* 123: 193–206.
- Loison A, Toigo C, Gaillard JM (2003) Large herbivore biodiversity in European mountain ecosystems: current status and challenges for the future. In: Nagy L (ed.) *Alpine Biodiversity – Pattern, Process and Change in Europe*, 351–366. Springer Verlag, Berlin, Germany.

- Maissels F (1988) *The Feeding Ecology of the Cyprus Mouflon Ovis orientalis Gmelin 1774, in the Paphos Forest, Cyprus*. PhD thesis, University of Edinburgh, Scotland, UK.
- Martínez T, Fandos P (1989) Solapamiento entre la dieta de la cabra montés (*Capra pyrenaica*) y la del muflón (*Ovis musimon*). *Acta Vertebrata* 16: 315–318.
- McInnis ML, Vavra M, Krueger WC (1983) A comparison of four methods used to determine the diets of large herbivores. *Journal of Range Management* 36: 302–306.
- Mendoza M, Janis CM, Palmqvist P (2002) Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. *Journal of Zoology* 258: 223–246.
- Miranda M, Sicilia M, Bartolomé J, Molina-Alcaide E, Gálvez-Bravo L, Cassinello J (2012) Contrasting feeding patterns of native red deer and two exotic ungulates in a Mediterranean ecosystem. *Wildlife Research* 39: 171–182.
- Mottl S (1960) *Mufloní zvěř, Biologie a chov*. Statni Zemědělské Nakladatelství, Prague, Czech Republic.
- Mysterud A, Sæther BE (2011) Climate change and implications for the future distribution and management of ungulates in Europe. In: Putman R, Apollonio M, Andersen R (eds) *Ungulate Management in Europe: Problems and Practices*, 349–375. Cambridge University Press, Cambridge, UK.
- Onderscheka K, Jordan HR (1974) Einfluss der Jahreszeit, des Biotops und der Äsungskonkurrenz auf die botanische Zusammensetzung des Panseninhaltes beim Gams-, Reh-, Muffel- und Rotwild. *Die Bodenkultur* 27: 202–217.
- Özütlü D (2009) *Évaluation du Processus d'Adaptation d'une Population Ré-Introduite de Mouflon (Ovis gmelinii anatolica) par l'Étude de sa Démographie et de son Écologie Spatiale*. PhD thesis, Université Toulouse 3 – Paul Sabatier, France.
- Pauthenet Y (1988) *Approche de la Stratégie Alimentaire des Ongulés en Estive (Vercors) – Apports de la Méthode d'Analyse Micrographique des Fécès*. PhD thesis, Université Joseph Fourier Grenoble 1, France.
- Peek JM (1974) A review of moose food habits studies in North America. *Le Naturaliste Canadien* 101: 195–215.
- Pérez-Barbería FJ, Gordon IJ (1999) The relative roles of phylogeny, body size and feeding style on the activity time of temperate ruminants: a reanalysis. *Oecologia* 120: 193–197.
- Pérez-Barbería FJ, Gordon IJ, Illius AW (2001a) Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants. *Oecologia* 129: 498–508.
- Pérez-Barbería FJ, Gordon IJ, Norens C (2001b) Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research* 3: 221–230.
- Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius AW (2004) The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proceedings of the Royal Society of London. Series B* 271: 1081–1090.
- Pfeffer P (1967) Le mouflon de Corse (*Ovis ammon musimon* Schreber, 1782). *Mammalia* 31 (suppl.): 1–262.
- Prins HHT, Fritz H (2008) Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. In: Gordon IJ, Prins HHT (eds) *The Ecology of Browsing and Grazing*, 179–200. Springer Verlag, Berlin, Heidelberg, Germany.
- Rameau J, Mansion D, Dumé G (1993) *Flore Forestière Française – Guide Écologique Illustré*. Institut Pour Le Développement Forestier, Paris, France.
- Redjadj C (2010) *Étude Inter- et Intra-Spécifique des Variations Spatio-Temporelles de l'Utilisation des Ressources Alimentaires au sein d'une Communauté de Grands Herbivores de Montagne*. PhD thesis, Université de Savoie, France.
- Rezaei HR, Naderi S, Chintauan-Marquier IC, Taberlet P, Virk AT, Naghash HR, Rioux D, Kaboli M, Pompanon F (2010) Evolution and taxonomy of the wild species of the genus *Ovis* (Mammalia, Artiodactyla, Bovidae). *Molecular Phylogenetics and Evolution* 54: 315–326.
- Rigaud P (1985) *Le Mouflon dans le Massif du Sancy*. PhD thesis, Ecole Nationale Vétérinaire, Lyon, France.
- Robert P, Escoufier Y (1976) A unifying tool for linear multivariate statistical methods: the RV-coefficient. *Journal of the Royal Statistical Society. Series C (Applied Statistics)* 25: 257–265.
- Rodríguez JL, Rodríguez JC, Ramos MT (1988) Autumn diet selectivity of the Corsica mouflon (*Ovis ammon musimon* Schreber, 1782) on Tenerife (Canary Islands). *Mammalia* 4: 476–481.
- Rodríguez Berrocal J, Molera Aparicio M (1985) Aprovechamiento de recursos alimentarios naturales: 1: contribucion al estudio de la dieta del gamo (*Dama dama*) y del muflon (*Ovis ammon musimum*) en el area ecologica de la Sierra de Cazorla. *Archivos de Zootecnia* 34: 3–25.
- Rodríguez Luengo J, Piñero J (1991) Autumn diet of the Corsica mouflon *Ovis ammon musimon* Schreber 1782 on Tenerife, Canary Islands. In: Bobek B, Perzanowski K, Regelin WL (eds) *Global Trends in Wildlife Management: Transactions of the 18th International Union of Game Biologists Congress, Jagiellonian University, Kraków, Poland, August 1987*, 137–140. Świat Press, Krakow-Warszawa, Poland.
- Sabados K, Manica M (1977) Potrava muflónej zveri v mimovegetacnom období Slovensku. *Folia Venatoria* 7: 81–93.
- Santin-Janin H, Garel M, Chapuis JL, Pontier D (2009) Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago. *Polar Biology* 32: 861–871.
- Schwartz C (1992) Physiological and nutritional adaptations of moose to northern environments. *Alces Supplement* 1: 139–155.
- Shackleton D, IUCN/SSC Caprinae Specialist Group (1997) *Wild Sheep and Goats and Their Relatives: Status Survey and Conservation Action Plan for Caprinae*. IUCN, Gland, Switzerland and Cambridge, UK.
- Storms D, Aubry P, Hamann JL, Saïd S, Fritz H, Saint-Andrieux C, Klein F (2008) Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology* 14: 237–250.

- Stubbe C (1971) Zur Ernährung des Muffelwildes – *Ovis ammon musimon* (Pallas, 1811) – in der Deutschen Demokratischen Republik. *Tagungsberichte – Deutsche Akademie der Landwirtschaftswissenschaften zu Berlin* 113: 103–125.
- Tixier H, Duncan P (1996) Are European roe deer browsers? A review of variations in the composition of their diets. *Revue d'Ecologie (La Terre et la Vie)* 51: 3–17.
- Todd J (1972) *A Literature Review on Bighorn Sheep Food Habits*. Technical Report, Special Report 27, Colorado Division of Game, Fish and Parks, and Cooperative Wildlife Research Unit, Denver, Colorado, USA.
- Trabalza Marinucci M, Capecci A, Riganelli N, Acuti G, Antonini C, Olivieri O (2005) Dietary preferences and ruminal protozoal populations in roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and mouflon (*Ovis musimon*). *Italian Journal of Animal Science* 4: 401–403.
- Uloth W (1972) To the history of the distribution, introduction and cross-breeding of the Tyrrhenis mouflon in Europe and oversea. *Acta Theriologica* 17: 412–413.
- Valentini A, Miquel C, Nawaz MA, Bellemain E, Coissac E, Pompanon F et al. (2009a) New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the *trnL* approach. *Molecular Ecology Resources* 9: 51–60.
- Valentini A, Pompanon F, Taberlet P (2009b) DNA barcoding for ecologists. *Trends in Ecology & Evolution* 24: 110–117.
- Van Wieren SE (1996) Browsers and grazers: foraging strategies in ruminants. In: *Digestive Strategies in Ruminants and Nonruminants*. PhD thesis, University of Wageningen, the Netherlands.
- Vavra M, Rice RW, Hansen RM (1978) A comparison of esophageal fistula and fecal material to determine steer diets. *Journal of Range Management* 31: 11–13.
- Vigne J (1992) Zooarchaeology and the biogeographical history of the mammals of Corsica and Sardinia since the last ice age. *Mammal Review* 22: 87–96.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Publications on mouflon diet not included in the statistical analyses.

Appendix S2. List of plant species and families found in the composition of mouflon (*Ovis gmelini musimon*) diet, in the 42 studies reviewed (Table 1 + Appendix S1).