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Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes

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How large herbivores track resource quantity and quality through time has formed the core of an abundance of literature on migratory populations in recent decades. Yet, relating foraging processes and habitat selection patterns in resident populations, where spatial heterogeneity of food resources is fine-grained and/or where the portion of edible plants (i.e. the foodscape) is low, is challenging. We addressed this issue in a mountain population of chamois *Rupicapra rupicapra*, an intermediate feeder, whose individuals do not migrate. We relied on a rare combination of data on habitat use of 50 GPS-collared females and data on the quantity (biomass) and quality (phenology) of edible resources in their landscape, derived from field sampling of vegetation, remote sensing and diet (DNA barcoding). The foodscape of the chamois was composed of a low proportion of the available biomass (<18%), including relatively high-quality plants, with low spatial covariation between plant phenology and biomass. Chamois avoided areas with a low edible biomass (where the intake rate may be too low) and focused on areas with plants at approximately the flowering stage, whatever the average plant phenological stage available. Due to this constant preference for flowering plants, home range selection ratios therefore shifted during the summer from a selection of more advanced plants in June to their avoidance in August. When the phenology scores of all plants available, rather than edible plants only, were considered, areas with relatively more advanced plants were selected all summer long. This exemplifies that, when traits from edible plants are different from those of all plants available, it is crucial to consider the actual foodscape to decipher forage and habitat selection processes. By integrating species-specific dimensions of resources in habitat selection studies, we believe understanding of the foraging processes will be improved.

Keywords: chamois, edible plants, habitat selection, northwest Alps, phenology, quality–quantity tradeoff, *Rupicapra rupicapra*

Introduction

An individual's foraging decisions in space and time largely influence its intake rate (Charnov 1976, Stephens and Krebs 1986), which subsequently drives long-term

individual performance (Gaillard et al. 2010). Upscaling foraging theories to longer time horizons has accordingly been the holy grail of behavioral ecologists (Senft et al. 1987, Mueller and Fagan 2008). The rapid advent of movement ecology and remote sensing in past decades (Nathan 2008, Pettorelli et al. 2011) has made progress in this direction possible by linking foraging models and habitat use with broad-scale movements in some large migratory herbivores in Africa (Fryxell et al. 1988, Boone et al. 2006) and in species facing temporally contrasted environments in the northern hemisphere (Festa-Bianchet 1988, Langvatn et al. 1996, Hebblewhite and Merrill 2009, Van Beest et al. 2010, Bischof et al. 2012). In these environments, herbivores move across areas that provide the best energy intake rate, which shifts in space over time according to broad-scale gradients of plant phenology, the so-called 'green wave' (Drent et al. 1978, Van der Graaf et al. 2006, Bischof et al. 2012, Aikens et al. 2017). As digestibility decreases and biomass increases during plant development, profitability for herbivores should be highest in areas where plant communities are, on average, at a medium developmental stage (Demment and Soest 1985, Hobbs and Swift 1985, Hansen et al. 2009). The behavioral response (in terms of diet and habitat selection) to spatiotemporal shifts in resource quantity and quality underpins the 'forage maturation hypothesis' ('FMH', McNaughton 1985, Fryxell 1991, Wilmshurst et al. 1995) and is the basis for models of migratory patterns in large herbivores (Bischof et al. 2012, Singh et al. 2012, Aikens et al. 2017).

Given that seasonal migrations at a broad scale can be explained by this connection between the spatiotemporal dynamics of resources and optimal foraging processes, the fact that not all species or all individuals of a given population migrate, even in seasonal environments or environments with strong altitudinal gradients, is puzzling (Fryxell et al. 1988, Chapman et al. 2011, Gaudry et al. 2015). In such cases, the challenge is to explain how optimal foraging processes and spatiotemporal variation of resources quality and quantity lead to the observed patterns of habitat selection at the scale of a home range, the location of which varies little over time. For resident individuals, the level of local heterogeneity in resource quality and quantity and the way individuals select foraging patches certainly play key roles (Shaw and Couzin 2013); that is, home range residency should occur when the temporal predictability of resources is high and the spatial heterogeneity of the resources is fine-grained (Mueller et al. 2011). In the mountains, for example, slope and aspect heterogeneities result in high diversity of habitat types and plant communities at a fine spatial scale (Dufour et al. 2006, Marchand et al. 2015a) and in a lower synchrony in plant growth than observed in relatively homogeneous and flat landscapes (Hebblewhite et al. 2008 in alpine shrubs, Duparc et al. 2012 in alpine grassland). In such situations, selection of the most profitable resources may occur in patches of both higher biomass and higher quality than average available patches, without having to track a 'green wave' (Hebblewhite et al. 2008).

Another line of enquiry to better understand how habitat selection results from optimal foraging processes is to identify how much of the 'green world' (Polis 1999) is actually edible for herbivores (Searle and Shipley 2008). Because body mass helps determine species' energy requirements and digestive abilities (Demment and Soest 1985, Hofmann 1989, Clauss et al. 2003), the gap between the characteristics of all available plants (biomass and functional traits) and the characteristics of edible plants should be wider for smaller species than for larger species. Indeed, the former are generally highly selective for high-quality and often sparsely distributed resources (Fryxell et al. 1988, Mysterud et al. 2012). The idea that resources should be defined in terms of species-specific edible resources in a landscape gave rise to the concept of a 'foodscape' (Searle et al. 2007, Marsh et al. 2014). Studying the role of the 'foodscape' (i.e. the distribution of resources as perceived 'through the taste buds' of the herbivore) in habitat selection should help understanding the role of diet selection in animal distribution at a broader spatial scale (Johnson 1980, Searle and Shipley 2008, Marchand 2013, Redjadj et al. 2014).

We investigated how the characteristics of the foodscape determined habitat selection by chamois *Rupicapra rupicapra* during the growing season in a population living in a mountain area (Bauges Massif, northern French Alps) characterized by highly diverse mountain pastures (Duparc et al. 2012). We expected chamois habitat selection to depend on the spatial covariation between quality and quantity of the edible forage available. If the covariation is weak or nonexistent, chamois may be able to select for areas containing both high quantity and good quality of edible resources; by contrast, if the covariation is strong, they may have to select for areas with intermediate values for both quality and quantity (Fryxell 1991, Hebblewhite et al. 2008). To test this hypothesis, we proceeded in three steps (Fig. 1). First, we defined the foodscape of chamois with a spatially and temporally explicit model collating a database on chamois diet (Bison et al. 2015), field data on vegetation biomass and phenology (Duparc et al. 2012), and remote sensing (Pettorelli et al. 2005). It allowed us to calculate the proportion of the available biomass that was edible for chamois and to compare the phenology advancement of edible plants to that of all plants. Second, we estimated the level of spatial covariation between the quality and quantity of edible resources and explored how this covariation changed during the growing season. Third, we calculated habitat selection ratios vis-à-vis the characteristics of the foodscape at the chamois home range scale (third-order selection, as defined in Johnson 1980), using a database on chamois female locations recorded with GPS collars (n = 50). Finally, to highlight the importance of accounting for diet selection to better understand resource selection patterns, we compared the habitat selection ratios provided by considering the foodscape (i.e. edible plants only) with ratios obtained by considering all plants available.
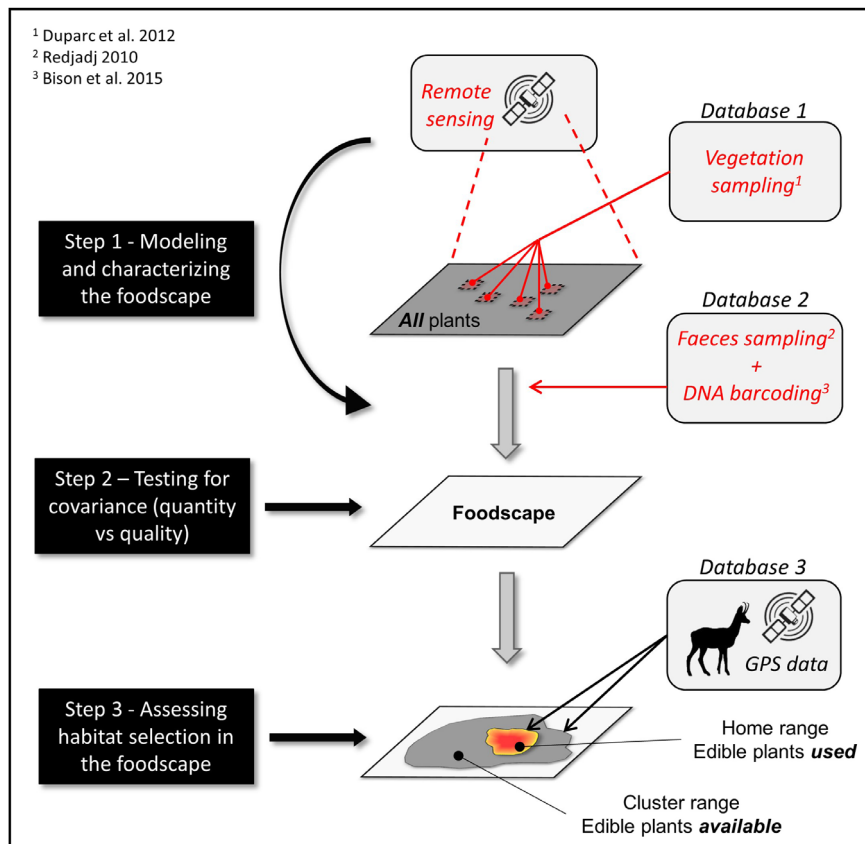
Figure 1. Hierarchical framework and datasets used to investigate selection for food resources by chamois. Gray rectangles with rounded corners represent databases, and black boxes, the methodological steps (see Statistical analyses section for details).

Material and methods

Study area

We conducted our study in the National Game and Wildlife Reserve (NGWR) of Bauges Massif, in the northern French Alps (45°40′N, 6°23′E; 900–2200 m a.s.l., 5200 ha). More than half of the area (56%) was covered by forests dominated by beech *Fagus sylvatica* and fir *Abies alba* groves. Alpine pastures covered 36% of the study area, and the remaining 8% were rocky areas (Lopez 2001). We defined eight plant communities in alpine pastures, based on dominant species: 'alder shrubs', 'alpenrose heaths', 'blue moorgrass–evergreen sedge swards', 'matgrass swards', 'mountain hay meadows', 'rusty sedge grasslands', 'tall herb community' and 'screes' (details in Duparc et al. 2012). The 'scree' category grouped all plant associations found on steep slopes and in disturbed habitats dominated by boulders and fallen rocks.

Study species

Chamois is a medium-sized dimorphic ungulate (average body mass of 30 kg for females and 40 kg for males, Garel et al. 2009), in which >80% of the females two years of age and older give birth annually to one young in late May (Loison 1995, Pioz et al. 2008). Chamois display a clan-like

organization, with loosely defined female and juvenile groups (Gerard and Richard-Hansen 1992, Crampe et al. 2007). We focused our study on the months following the birth peak (June–August, Loison 1995), which is a critical period for mountain ungulates (Pettorelli et al. 2007, Hamel et al. 2009) because of the high energy requirements for lactation and storage of fat reserves before winter (Clutton-Brock et al. 1989, Stearns 1992, Jönsson 1997, Richard et al. 2017). In our population, females use similar home ranges from year to year (Loison et al. 1999, 2008) and display little seasonal altitudinal migration during June through August (the maximal elevational change occurred between June and July with only 11.7 ± 10.9 m).

Databases

Database of available plants from field sampling (database 1, Fig. 1)

From 2007 to 2010, we measured green biomass, plant species composition (using BOTANAL technique, Tothill et al. 1992, Redjadj et al. 2012) and plant phenology stages in all plant communities. Using a hierarchical random sampling design, we sampled 147 plots, stratified by the area of each plant community (see details in Duparc et al. 2012), from May to the end of October (Supplementary material Appendix 1 Table A1-1). From these field works,

we estimated the green biomass per plant community during the 2007–2010 growing seasons at the 25×25 m level.

Plant development stages should be indirect proxies of plant quality, as the forage digestibility and nutrient availability (nitrogen, phosphorus and carbohydrates) decreases with the advancement of plant phenology (Demment and Soest 1985, Hobbs and Swift 1985, Hebblewhite et al. 2008). This negative covariation, however, may not hold during the earliest stages of development, i.e. right after emergence (Terry and Tilley 1964, Chapin and Shaver 1989, Mårell et al. 2006), but is a pattern to consider when interpreting phenology as a quality proxy. In our study, we identified four phenological stages – growth, flowering, appearance (fruiting) and loss of fruit (senescence) – which were coded 1–4, respectively (hereafter called 'phenology scores'). We estimated these phenology scores for plant species sampled in 62 plots (selected among the 147 for biomass sampling; Duparc et al. 2012; Supplementary material Appendix 1 Table A1-2) from May to October. A plant species was attributed to a given stage when more than 10% of individuals in the community reached this stage. We calculated the community weighted mean (CWM) of the plant phenology scores (Lavorel et al. 2008, Duparc et al. 2012), i.e. the mean of the species' phenology scores, weighted by the relative abundance of each species in the community, as a proxy of plant development over time (Hanley and McKendrick 1983, Arzani et al. 2004, Mårell et al. 2006) for the study area during the 2007–2010 period.

Diet dataset from DNA barcoding (database 2, Fig. 1)
We collected 297 feces (47% from females and 75% from adults) in the NGWR from April to August 2007 and 2008, either in the field (79%) or directly from trapped chamois (21%, Redjadj 2010). For feces collected in the field, we relied on a 500 m resolution grid to ensure our sampling design was representative of the population range. Only feces covered with animal mucus and free from coprophagous insects, e.g. dung beetles, were harvested to insure sample freshness (Redjadj 2010, Rayé et al. 2011, Bison et al. 2015). The dietary composition of the feces was determined using DNA metabarcoding techniques (Rayé et al. 2011, Bison 2015, Bison et al. 2015). We focused on plants for which the proportions of DNA sequences were >2.5% of the total number of sequences in the feces with possible chimeras and those sequences with PCR and sequencing errors being discarded (Rayé et al. 2011, Bison 2015, Bison et al. 2015). This 2.5% threshold was chosen because it marked a rupture in the frequency distribution of the sequences (Pompanon et al. 2012). Finally, the remaining 74 plant taxa were dominated by evergreen shrubs, deciduous shrubs, forbs and leguminous species (species list in Supplementary material Appendix 2). The occurrence of a plant species was calculated as its proportion of presence in all feces sampled for a given season.

Chamois home range database from GPS collars (database 3, Fig. 1)
We trapped 50 adult females during spring and summer for the years 2005 through 2013 using falling nets baited with artificial salt licks in two alpine grasslands (n = 29 and n = 21) 9.9 km apart and between which no exchange occurs in female chamois (Loison et al. 2008). We fitted animals with GPS collars from which we retrieved one daily location (over the different schedules used during the study period). We screened GPS data for positional outliers (n = 262; 1.21% of the full data set) based on unlikely movement characteristics ($\Delta = 5000$ m, $\mu = 4000$ m, $\alpha = 90\%$ quantile of movement speed from a focal individual, $\theta = -0.90$, Bjørneraas et al. (2010). Then, we calculated 90% home ranges (see methodological details in Supplementary material Appendix 3) for all individuals per year and per month. The total number of monthly home ranges estimated for the study period was 212, of which 60 individuals were trapped in June, 64 in July, and 88 in August, with some females being monitored for two years. The monthly home ranges constituted the home range database, defining the area used by each marked female each month.

The annual home ranges were used to define clusters of females, i.e. females with strongly overlapping home ranges all year long (see details on clustering in Supplementary material Appendix 3). The area potentially available for a female during the growing season was the aggregation of all the monthly home ranges used by individuals belonging to the same cluster during the June–August period, and this area is hereafter referred to as the cluster range.

Statistical analyses

Step 1. Modeling the biomass and phenology of all plants and of edible plants (foodscape) by collating databases 1 and 2 and environmental data (Fig. 1)

Our goal was to model forage biomass and phenology during the entire study period (2003–2014). To this end, we spatially and temporally paired each empirical biomass estimate collected in 2007–2010 with the predicted values of NDVI at the same spatial location and date (Supplementary material Appendix 1 for NDVI computing details). Then, we performed nonlinear mixed-effects models to fit green biomass for each plant community, with NDVI as a fixed effect and year as a random effect (Pinheiro and Bates 2000). Green biomass was log-transformed to achieve normality. We used the four-parameter logistic function (Nelder 1961) because it allowed us to set the horizontal asymptote on the left at 0 (a; for low values of x) and the horizontal asymptote on the right at the 95% quantile (b; for large values of x). The use of the 95% quantile as an upper limit allowed us to avoid overestimation in prediction with the highest NDVI values.

$$y = a + \frac{b - a}{1 + e^x} \qquad (1)$$

We used a similar methodology to model the variation in phenology scores according to the degree-days values (fixed effect in nonlinear mixed effects models; Billings and Mooney 1968, Cannell and Smith 1983, Chuine 2000, Körner 2003, Cleland et al. 2007). The horizontal asymptote values on the

left (a) and on the right (b) were 1 and 4, respectively, i.e. the limits of the possible phenology scores according to our coding. Degree-days were calculated with a base temperature of 0°C (Pastor and Post 1985) from the daily temperature average at the Lescheraines weather station (Meteo France; 590 m a.s.l.) in Bauges Massif.

We used the models fitted during the 2007–2010 period to predict weekly values of biomass and daily phenology scores at the 25×25 m resolution for the whole study area and study period (June–August for 2003–2014 period). To assess the accuracy of our predictive models, we applied the cross-validation method with a training set of 80% of the dataset randomly sampled and a test set on the remaining 20%. We calculated the adjusted R^2, mean absolute error (MAE) and coefficient of variation of MAE (CVMAE) between predicted and observed values to estimate the performance of our models (López-Moreno et al. 2008, Choler et al. 2011). This procedure was repeated 500 times (see details in Supplementary material Appendix 1).

To determine the biomass and phenological scores of the plants actually eaten by chamois, we relied on the same models but predicted these values only for the subset of edible plants within each plant community and weighted the plant abundance by its occurrence in the diet (databases 1 and 2). Then, we tested whether the mean availability of food resource for chamois changed from month to month in terms of biomass and plant quality for all plants or for edible plants only using a linear mixed model with month as the fixed effect and year as the random effect (number of years: $N_{June} = 8$, $N_{July} = 9$, $N_{August} = 8$). Finally, to assess the diet selectivity of the chamois per month, we calculated the mean and 95% CI of differences in availability between all plants and edible plants only.

Step 2. Testing for spatial covariation between forage quality and quantity available in cluster ranges

We used major axis regression (MA) to compute the monthly covariation between biomass and phenology scores of edible plants estimated in every pixel of the six spatial clusters (Supplementary material Appendix 3) identified in the studied population. We used a permutation test to determine the significance of the slopes of MA (N permutations = 1000, Legendre and Legendre 2012).

Step 3. Identifying the role of edible resource biomass and quality in habitat selection at the monthly home range scale

We first estimated selection ratio (Savage 1931, Manly et al. 2002, Holbrook et al. 2019) vis-à-vis edible biomass or phenology for each individual/month as $w_i = o_i / \pi_i$, where o_i is the average value of edible biomass or phenology in the 90% monthly home range of the individual i, and π_i is the average value (edible biomass or phenology score) in its cluster range (n = 212 chamois-month-year). Selection ratios >1 would indicate higher values in the home range compared to the available range, while selections ratios <1 would indicate relatively lower values. To visualize whether covariation existed between the selection for edible biomass and selection for plants with higher phenology scores, and whether this covariation changed through time, we then plotted selection for biomass against selection for phenology scores for each month. We also repeated this analysis with the biomass and phenology of all plants, not only the edible one, to check whether it is worth identifying the foodscape for understanding resource selection patterns at the third order of selection for this species.

To gain further insight on the selection behavior of individuals in their home range, we also split the biomass and phenology values in three classes based on month-specific percentiles of these two variables: 0–33% (low biomass or relatively low month-specific CMW phenology scores), 34–66% (medium biomass or average month-specific CMW phenology scores) and 67–100% (high biomass or relatively high month-specific CMW phenology scores). Then, we calculated selection ratios (Savage 1931, Manly et al. 2002, Holbrook et al. 2019) as $w_{ij} = o_{ij} / \pi_{ij}$, where o_{ij} is the proportion of pixels of class j in the 90% monthly home range of individual i and π_{ij} is the proportion of pixels of class j in the available cluster range of the individual i (n = 212 chamois-month-year).

We tested whether selection for food resources changed from month to month by implementing mixed-effect models with selection ratio (vis-à-vis biomass or phenology, on average or in classes; n = 212) as the response variable and year, cluster and individual as random effects (Bates et al. 2015, package 'lme4' in R). We compared the null model against the model including months as a fixed effect using Akaike's information criterion (AICc), with second-order adjustment to correct for small sample bias (Burnham and Anderson 2002, Barton 2018, package 'MuMIn'). Following Burnham and Anderson (2002), models were ordered from the best to the least supported model (lowest to highest AICc). We considered nonoverlapping 95% confidence intervals with 1 (no selection) indicating a significant selection for (if $w > 1$) or against (if $w < 1$) the focal variable. We considered nonoverlapping 95% confidence intervals between months as significantly different.

Results

Modeling the biomass and phenology of all plants and of edible plants (foodscape) (Step 1)

The biomass of plants that are edible for chamois (estimated in the field) increased with increasing NDVI values in all plant communities (loglikelihood ratio test, $p < 0.02$). The performance of models in predicting edible biomass in each plant community based on NDVI values was consistent for all plant communities except 'scree', with the amount of variance explained by each model (R^2) ranging from 0.36 to 0.69 (see details for each plant community in Supplementary material Appendix 1). The R^2 for 'scree', however, was much lower ($R^2 = 0.08$). The error on the predicted amount of edible biomass (CVMAE) was $13.7 \pm 3.9\%$ on average

Table 1. Estimated mean and 95% confidence intervals for biomass values and phenology scores for the study site, considering all plants or edible plants only and their proportional differences, per month.

	Mean [CI 95%] total biomass (g m^{-2})		Mean [CI 95%] edible biomass (g m^{-2})		Mean [CI 95%] inedible total biomass		Mean [CI 95%] percent inedible	
June	123.3	[107.6, 138.9]	20.5	[17.3, 23.6]	102.8	[89.3, 116.3]	83.4%	[72.4, 94.3]
July	137.0	[126.1, 148.9]	23.9	[22.0, 25.7]	113.1	[102.9, 123.4]	82.6%	[75.1, 90.1]
August	115.4	[95.4, 135.3]	20.4	[16.8, 24.0]	95.0	[78.7, 111.3]	82.3%	[68.1, 96.4]

	Mean [CI 95%] total phenology		Mean [CI 95%] edible phenology		Delta [CI 95%] total-edible phenology		Delta [CI 95%] in percent of total phenology	
June	1.52	[1.34, 1.70]	1.43	[1.25, 1.62]	0.09	[0.05, 0.12]	5.9%	[3.3, 7.9]
July	2.56	[2.41, 2.71]	2.42	[2.26, 2.57]	0.14	[0.11, 0.16]	5.4%	[4.3, 6.3]
August	3.42	[3.35, 3.49]	3.31	[3.23, 3.39]	0.11	[0.10, 0.12]	3.2%	[2.9, 3.5]

(9.8 ± 0.8% without 'scree' category). The models forecasting the total biomass in each plant community, rather than of the biomass of edible plants only, had similar predictive performance (R^2 ranging from 0.31 to 0.64 and average CVMAE of 7.3 ± 1.1% without 'scree').

Similarly, in all plant communities, the CWM-phenology scores of the edible plants (estimated in the field) increased during the growing season, i.e. with increasing day-degrees (loglikelihood ratio test, $p < 0.001$). The performance of the models in predicting phenology scores in each community based on the day-degrees values was high in all plant communities (R^2 from 0.73 to 0.86), with low prediction errors (CVMAE = 15.8 ± 2.8% on average). The models forecasting the average phenology scores (CWM phenology scores) for all plants available within each community, rather than for edible plants only, had a similar predictive performance (R^2 ranging from 0.76 to 0.93; CVMAE = 13.8 ± 2.5%).

Using these models that calibrated 2007–2010 field measurements of biomass and phenology to NDVI and day-degrees respectively, we predicted biomass (based on NDVI values) and phenology scores (based on day-degrees) of edible plants or of all plants over the whole study area for the whole study period (2003–2014). We could thereafter estimate average biomass and phenology scores at the cluster or individual home range levels per month and year. The average biomass (averaged over all clusters combined) was stable during the three months of the growing season (Table 1, Fig. 2), both when considering all plants (mean: 125.7 ± 4.2 g m^{-2}; ΔAICc between null model and model with month effect: 0.18) or edible plants only (21.7 ± 0.7 g m^{-2}; ΔAICc: 0.24). As expected, the CWM-phenology scores (averaged over all clusters combined) increased markedly from June to August (Table 1, Fig. 2; ΔAICc between null model and model with month effect: 83.1 and 84.6, for all and edible plants respectively).

The biomass of edible plants was only 17.2 ± 0.9% of the total biomass available, and this proportion remained stable from June to August (Table 1). Chamois selected plant species of relatively earlier phenology stages than the average of all plants available (between 3% and 6% lower, Table 1). The foodscape of chamois was therefore composed of plants with relatively slow development and low biomass.

Testing for spatial covariation between edible forage quality and quantity available in cluster ranges (Step 2)

Phenology scores and biomass values of edible plants of each pixel significantly covaried in all months (June: β = 0.1137 ± 0.0009, $p < 0.001$; July: β = 0.0306 ± 0.0008, $p < 0.001$ and August: β = −0.0018 ± 0.0005, $p < 0.001$) mostly due to the very large sample size available (>500 000 pixels). However, biomass and phenology scores both strongly increased only at the start of the growing season (June), when a 100-fold increase in biomass led to a 30.6% increase in the phenology score. By contrast, in July and August, i.e. when most plants reached advanced phenology stages, the 100-fold increase in biomass was poorly related to a change in the phenology score (5.5% and −0.2%, respectively; see also R^2 in Fig. 3).

Chamois habitat selection in their foodscape (Step 3)

Plotting selection ratios for biomass versus selection ratios for phenology (Fig. 4a–b) unveiled different selection patterns from June to August (ΔAICc between the null model and the model with month effect: 20.65). In June, biomass did not play a significant role in explaining home range positioning in the available range (Fig. 4b), despite a slight avoidance of areas with the lowest biomass values (Fig. 5a–b). Instead, selection was strong vis-à-vis phenology scores (Table 2): individual monthly home ranges were positioned in areas where edible plants had higher phenology scores (i.e. more advanced plants) than the average score in their available cluster range. Average CWM-phenology scores in cluster ranges during this month indicated that plants were on average between the emergence and flowering stages (Fig. 5c), but chamois selected areas where edible plants were close to flowering (Fig. 5d).

In July and August, monthly home ranges were positioned in areas with more edible biomass than available in cluster ranges (Fig. 4b). These high biomass values in individual home ranges resulted from the avoidance of areas of low edible biomass rather than a preference for areas of high edible biomass (Fig. 5b, Table 3).
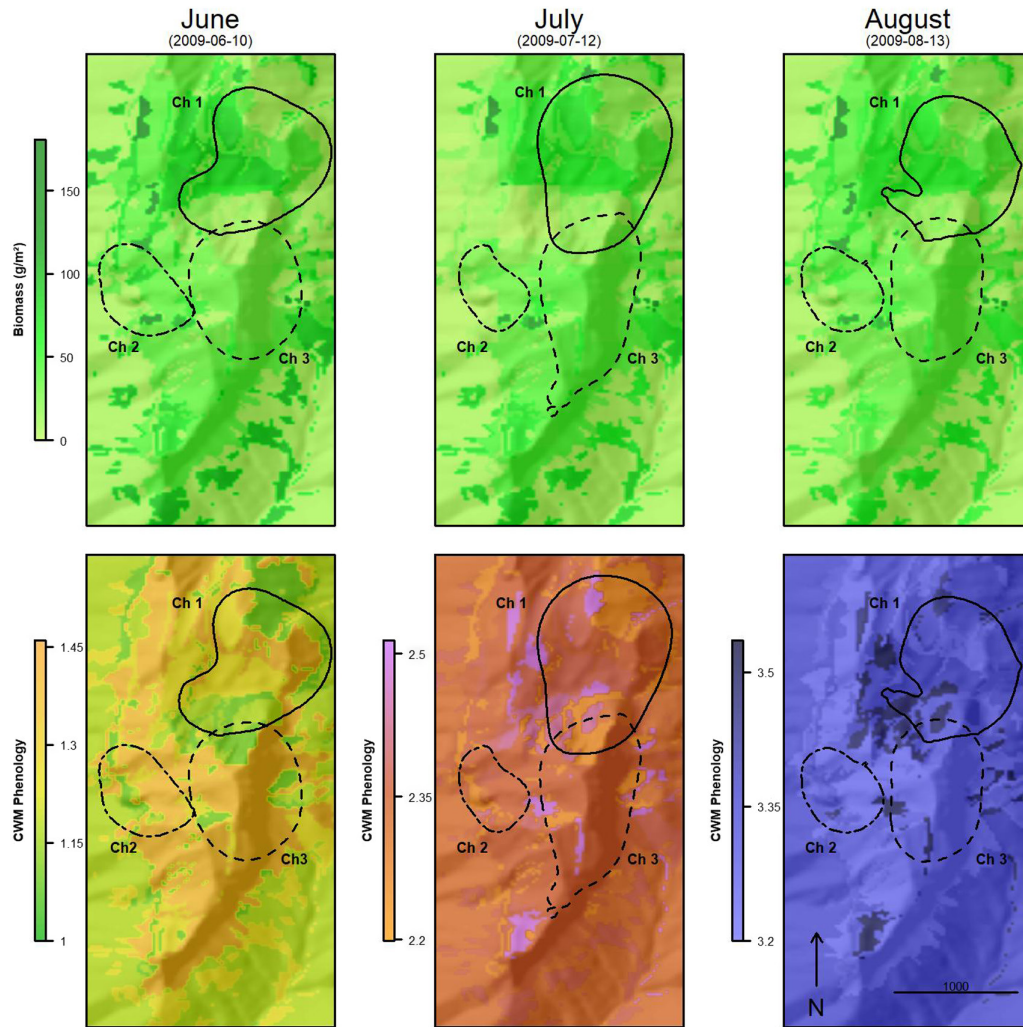
Figure 2. Mapping of a part of the study site where colors are the fitted values for biomass and community weighted mean phenology (CWM phenology) for plants edible for chamois (foodscape) for three dates during the summer period (middle of June, July and August). Solid, dashed and dot-dash polygons represent monthly 90% home range of three female chamois surveyed for this study (Ch 1–3).

No selection regarding phenology scores occurred in July when available edible plants were between flowering and fruiting (Fig. 5c): the average CWM-phenology scores in the available ranges and in the individual home ranges were similar (Fig. 4b). This lack of selection however masked a kind of 'stabilizing' selection, home range being preferentially in areas with plants within the 33–66% percentiles of the phenology scores (Fig. 5d).

In August, chamois selected areas where edible plants had lower phenology scores (i.e. less advanced plants) than available on average in their cluster ranges (Fig. 4b). While the average CWM-phenology scores in available ranges indicated plants between fruiting and senescence (Fig. 5c), home ranges included a much larger proportion of areas with less advanced edible plants (Fig. 5d).

To sum up, selection ratios for the different categories from June to August unveiled that individuals consistently located their home ranges where edible plants were mostly around the flowering stage (Fig. 5d), which translated into

different monthly selection values due to the advancement of plant phenology during the growing season (Fig 5c). In addition, chamois home ranges had higher biomass than available in their available cluster range (but in June), as a consequence of consistently avoiding areas with low biomass (Fig. 5b).

Comparing selection patterns considering all plants or edible plants only

We found comparable results concerning the selection of biomass in monthly home ranges when considering all plants instead of edible plants only (Supplementary material Appendix 4): biomass in home ranges was higher than in the corresponding cluster ranges (Fig. 4c). However, we found marked discrepancies between both approaches concerning selection of phenology in monthly home ranges. When considering all plants, chamois were found to select areas where plants had higher phenology scores than on average in the available range, whatever the month (Fig. 4c, Supplementary
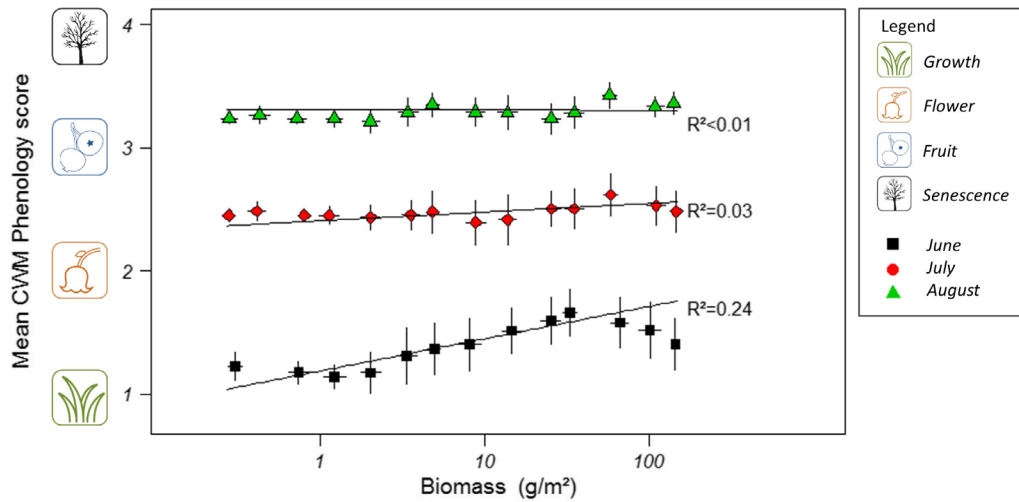
Figure 3. Monthly relationships between phenology and biomass (log-transformed) for plants edible for chamois. Vertical and horizontal error bars represent standard deviations of biomass and community weighted mean phenology scores (CWM phenology), respectively (biomass data were binned for the sake of readability). The solid lines correspond to the major axis regression.

material Appendix 4). The tracking of a specific phenology stage (close to flowering, Fig. 5d) through the growing season, as observed when relying on the foodscape of chamois, would thus have been overlooked as a criterion for habitat selection by considering all plants instead of edible plants only.

Discussion

The combination of data on the actual foodscape of chamois with monthly home ranges of GPS-monitored individuals revealed contrasting habitat selection behavior during the growing season vis-à-vis the relative importance for resource quantity (i.e. through biomass) and quality (i.e. through phenology). We posit that these selection patterns indicate two combined processes: 1) the selection of areas with biomass

over a minimum threshold, probably because a too low a biomass limits intake rate, and 2) the use of areas with plants within a close range of a target phenology score (flowering), the outcome of which, in terms of selection, depend on the advancement of plants in the available range. These selection patterns were enabled by hardly any spatial covariation between edible plant phenology and biomass, a consequence of the high local plant diversity and the diet of the chamois. As estimating the resources available to a given herbivore species is far from trivial (Pettorelli et al. 2005, Pettorelli 2013, Schweiger et al. 2015), we delve below into the relevance of the phenology scores as proxies of resource quality. We further argue that describing the actual foodscape rather than the distribution of resources is crucial for a better understanding of the connection between foraging processes and habitat selection, especially for sedentary and/or small
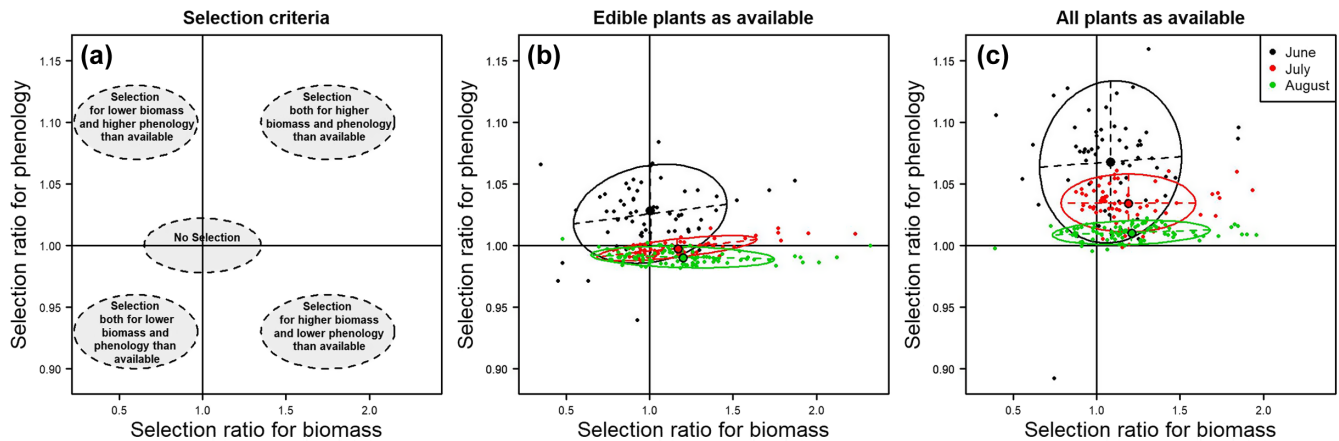

Figure 4. Monthly covariation between selection ratios for phenology and selection ratios for biomass (both considered as continuous variables), with an interpretation panel (a), considering edible plants only (b) or all plants (c). Ellipses are centered on mean values of x- and y-variables and include 75% of observations (n = 212). The horizontal and vertical axes (=1) represent the absence of selection for biomass and phenology, respectively.
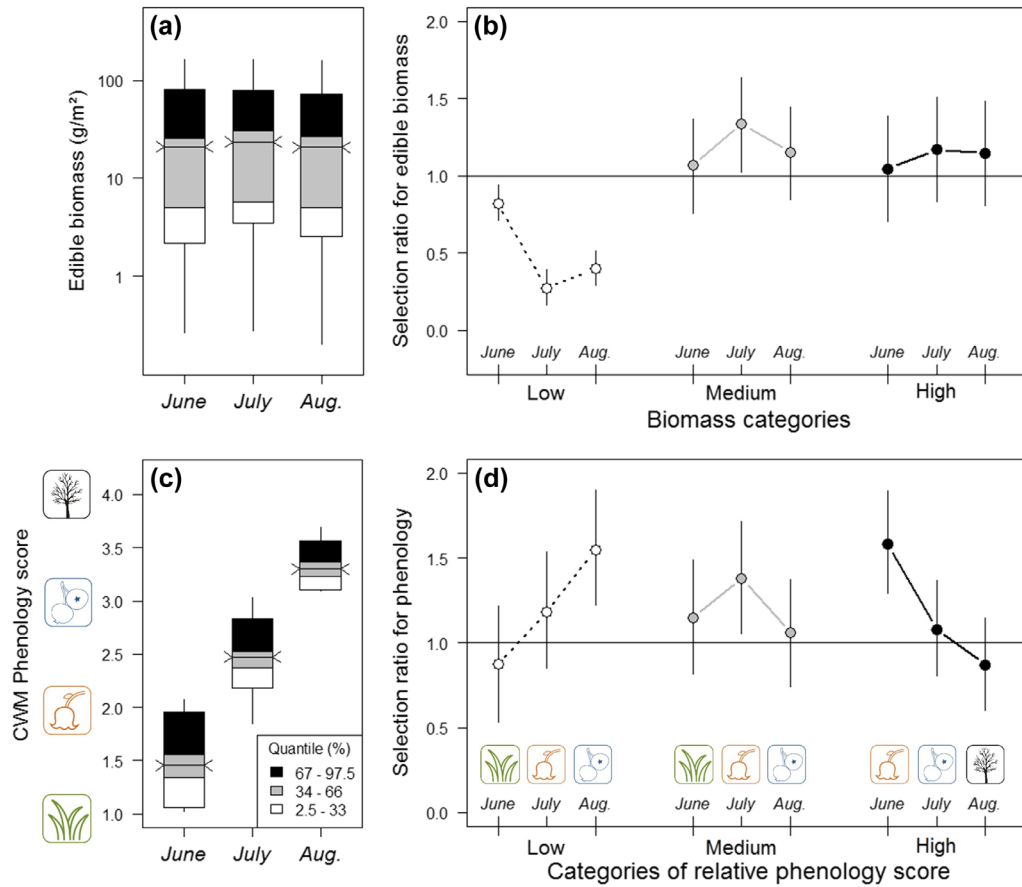
Figure 5. Monthly distributions of (a) biomass and (c) community weighted mean phenology scores (CWM phenology) of plants edible for chamois (foodscape). Cursor and vertical bars represent the mean and the range of each variable, respectively. Selection ratios (fitted values from best model with 95% confidence intervals) per month for biomass (b) and CWM phenology (d) categories (low, medium, high) of edible plants (foodscape). The horizontal bar (=1) represents the absence of selection. Estimates and confidence intervals on the selection ratios were obtained from mixed-effects models with the month as fixed effect, and including year, cluster and individual as random effects (n = 212).

mixed-feeder species living in highly heterogeneous landscapes (Duparc et al. 2012, Schweiger et al. 2015), which have been less scrutinized than species tracking the green wave over large spatial scales (Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017).

Table 2. Fitted values and 95% confidence intervals of selection ratios (ω) calculated using monthly biomass and phenology values of edible plants for chamois (foodscape) in Bauges Massif (northern French Alps). Significant selection ratios ω, i.e. for which 1 is not included in the confidence interval (CI 95%), are in bold (see also Fig. 4).

	ω	CI 95%
Mean biomass		
June	1.03	[0.85, 1.21]
July	**1.21**	**[1.03, 1.39]**
August	**1.22**	**[1.04, 1.39]**
Mean phenology		
June	**1.025**	**[1.019, 1.030]**
July	0.997	[0.992, 1.002]
August	**0.990**	**[0.985, 0.995]**

Table 3. Comparison of models with or without monthly variation for biomass values and phenology scores of edible plants, for each of the classes (low, medium, high). df: degree of freedom; AICc: second-order Akaike information criterion; ΔAICc: differences in AICc between the best supported model (lowest AICc; in bold) and others (see also Fig. 5).

Categories	Model	df	logLik	AICc	ΔAICc
Biomass					
Low	**month**	7	**−62.851**	**140.3**	**0**
Low	null	5	−105.976	222.2	81.99
Medium	**month**	7	**−167.269**	**349.1**	**0**
Medium	null	5	−172.185	354.7	5.58
High	**null**	5	**−168.541**	**347.4**	**0**
High	month	7	−167.478	349.5	2.13
Phenology					
Low	**month**	7	**−70.867**	**156.5**	**0**
Low	null	5	−102.017	214.5	57.92
Medium	**month**	7	**−202.192**	**419**	**0**
Medium	null	5	−206.009	422.3	3.36
High	**month**	7	**−114.227**	**243.1**	**0**
High	null	5	−135.848	282	38.93

9

Evidence for a threshold in selection patterns for biomass

Most studies performed at broad spatiotemporal scales found that short-term energy gains are generally maximized at intermediate values of forage quantity and quality as a result of the negative relationship between these forage characteristics (the forage maturation hypothesis, Fryxell 1991, Hebblewhite et al. 2008). However, Fryxell (1991) hypothesized that, unlike grazers, browsers (and intermediate feeders such as chamois) could depart from FMH-like behavior because they feed more on dicots, which are intrinsically of better digestibility than monocots (Owen-Smith and Novellie 1982). Our results are in accordance with this hypothesis, as chamois consistently avoided areas with a relatively low edible biomass (easily explained by a too-long searching time and too low intake rate in such areas, Spalinger and Hobbs 1992, Gross et al. 1993), but not the areas of high biomass (Fig. 4). In July and August, when biomass and phenology scores covaried only weakly, the most surprising result was actually the lack of a stronger selection of areas with high biomass of edible plants. We posit here that, in these medium-altitude pastures of high productivity (Körner 2003), the intake rate may be nonlimiting above a threshold biomass, and that this threshold biomass may be quite low for chamois, i.e. corresponding to the medium biomass category of edible plants. This is consistent with chamois being an ungulate species of relatively small size (Fritz et al. 2003), hence with low absolute daily energy requirements, a relatively limited ability to digest fibers (Demment and Soest 1985, Clauss et al. 2003), and a strong selectivity level (less than 18% of the standing biomass was edible for chamois whatever the month in our study, see Table 1). An alternative (and nonexclusive) hypothesis for the lack of a stronger selection of areas with high biomass of edible plants is that searching and handling time may be longer in areas with dense vegetation (high biomass) than in areas with medium biomass (Van de Koppel et al. 1996, Mezzalira et al. 2017).

Evidence for a target phenology score and implications for using phenology scores as a proxy of resource quality

Plants close to the flowering stage appeared to be the targeted phenology stage throughout the summer suggesting that plants in such a stage could be of higher nutritional quality for chamois than the earliest stages (Terry and Tilley 1964). Although often considered in the literature as representing the best forage quality (Hanley and McKendrick 1983, Van Soest 1994, Asaadi and Khoshnood Yazdi 2011), the earliest stages may suffer from a lower concentration in nutrients (e.g. carbohydrates and nitrogen) as compared to latter phenology stages, because of the lag in the plant's re-allocation of nutrients from the root systems (Hanley and McKendrick 1983, Chapin and Shaver 1989, Mengel et al. 2001, Körner 2003, Mårell et al. 2006). The different values of the selection

ratios toward phenology therefore correspond to similar preferences of chamois whatever the month, but in contexts where available, edible plants change in quality over time. For instance, in August, when most plants were senescent, chamois selected areas with plants of relatively lower phenology scores, close to flowering, as expected and found elsewhere (Klein 1990 in reindeer, Albon and Langvatn 1992 in red deer, Van Beest et al. 2010 in moose). These monthly varying patterns are akin to patterns found when studying animal functional response, i.e. selection for a preferred resource or habitat varies with varying availability of the resource or habitat (Mysterud and Ims 1998, Mauritzen et al. 2003, Pellerin et al. 2010, Duparc et al. 2019a, Holbrook et al. 2019).

That chamois seek a target phenology stage (flowering), which challenges our initial hypothesis that individuals would systematically prefer edible plants with relatively delayed development. This finding also indicates that, in June, when the covariation between biomass and phenology scores is positive, the chamois perceive a foodscape where quantity and quality covary positively in space, which also explains why the FMH cannot hold here. Although direct measurements of edible plant quality in the field, on large areas and over months and years, would be difficult, a knowledge gap exists in what constitutes forage quality for different herbivore species from individual plants to plant communities that constitutes herbivore habitats (Bruinenberg et al. 2002, Bumb et al. 2016). Our approach that collates data on diet, field sampling of vegetation composition, biomass and phenology, and remote sensing (Fig. 1) paves the way for delving into the complexity of habitat and resource selection seen through the species-specific taste buds of individuals.

Identifying the proper cues of habitat selection: the importance of the foodscape

Only a few habitat selection studies accounted for species-specific characterization of the foodscape (Moore et al. 2010, Marsh et al. 2014) because getting data on these species-specific ecological traits in the wild is tricky. This explains why most studies rely on broad habitat types (open versus closed in the most simplistic cases) or focus on a limited number of edible plants (Pellerin et al. 2010, Van Beest et al. 2010). In the case of species like chamois that consume only a limited and nonrandom part of the available plants (feeding from 17% of the available biomass, Table 1, Demment and Soest 1985, Hofmann 1989, Clauss et al. 2003), assessing the spatiotemporal variation in quantity and quality of the edible portion of the landscape appears essential. Importantly, we would have misinterpreted the foraging selection processes underlying habitat selection if we had relied on selection ratios for phenology based on all plants, as those ratios indicated a preference for areas with plants in more advanced phenology stages during all months. Surprising results, such as those in Schweiger et al. (2015), where chamois were found to forage in areas with plants of overall lower nitrogen content than

ibex or red deer, may likewise be explained by the fact that nitrogen content was estimated on all available plants, most of which may not be eaten by chamois. Acknowledging that in a given landscape, coexisting species have different foodscapes should also contribute to better explaining coexistence mechanisms and the lack of apparent competition observed even when species overlap spatially (Bertolino et al. 2009, Darmon et al. 2012, Redjadj et al. 2014, Bison et al. 2015).

Here, we focused only on the foraging components of space use and selection during summer and left out the other constraints that also influence herbivore spatial behavior (Festa-Bianchet 1988, Mysterud and Østbye 1999, Dussault et al. 2005, Hamel and Côté 2007, Marchand et al. 2015b). Females during this period may, for instance, not exploit the best quality food due to predator avoidance (Caro et al. 2004, Ruckstuhl and Neuhaus 2006, Nesti et al. 2010, Bjørneraas et al. 2012, Ferretti et al. 2014). Nevertheless, chamois females managed to improve their foraging conditions through a selective positioning of their home range (third order of selection, Johnson 1980), indicating that food resources was a predominant determinant of habitat selection for females during summer. Likewise, even though temperature imposes thermic constraints on habitat selection during the summer months (Mason et al. 2014), these constraints were still not strong enough to hamper home range selection for the most rewarding food resources.

Conclusion

Habitat use results from multiscale and multifactorial processes (Senft et al. 1987, Bailey et al. 1996, Van Beest et al. 2010), and its outcome in terms of individual movement and distribution depends on how landscapes of fear and foodscapes vary in space and time (Mueller and Fagan 2008). Here, focusing on resident chamois feeding on a small portion of the available plants and living in a habitat offering high local plant diversity, we demonstrated how selection behavior of a large herbivore shifted according to the spatiotemporal variation of the food resources. Understanding residency/nomadism/migration depends on habitat heterogeneity patterns and predictability (Mueller and Fagan 2008, Schick et al. 2008, Shaw and Couzin 2013, Peters et al. 2017) and should improve by performing comparative analyses of case studies relying on a thorough assessment of species-specific landscapes of fear and foodscapes. In this paper, we focus on the third order of selection (the home range placement, Johnson 1980) to exemplify the need for specific foodscape assessments to understand the forage selection process. However, at the finer scales (4th orders), knowledge of the foodscape should also be an essential parameter to delve into understanding of the spatial behavior of a large herbivore. New technologies (remote sensing: Pettorelli et al. 2011, DNA barcoding: Pompanon et al. 2012 and GPS collars: Kays et al. 2015), if properly calibrated with field data (plant composition, phenology and biomass, and species-specific diets), open new avenues for advancement.

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