Research Article

Habitat-Related Variation in Carcass Mass of a Large Herbivore Revealed by Combining Hunting and GPS Data

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ABSTRACT Studies on habitat–performance relationships that require joint data on fitness and habitat use are still scarce in long-lived species. Using data from a southern French population of Mediterranean mouflon (*Ovis gmelini musimon × Ovis* sp.), we proposed an original approach for gaining information on this relationship by combining a fitness proxy (i.e., carcass mass) collected on harvested rams ($n = 257$) with knowledge on habitat use obtained from other rams ($n = 13$) fitted with Global Positioning System (GPS) collars. We first evaluated habitat characteristics encountered by harvested animals in hypothesized home ranges corresponding to circles centered on harvest locations. We set circle size to equal an average ram home range. We found that the carcass mass of harvested individuals decreased with aspect diversity (−16.0% from home ranges with the lowest to the highest diversity), mean slope (−9.3% between flat home ranges and steep ones), and decreasing abundance of open areas (−11.3% between the most and the least open areas). We then tested the robustness of our results by simulating circles with variable sizes and whose centers were randomly located around each harvest location. We found similar results confirming that some habitat characteristics that may be related to resource abundance and spatial structure were important drivers of ram carcass mass in this population. Finally, we showed that simulated circles of variable sizes and centered on GPS locations captured well the habitat composition of home ranges of GPS-collared rams. Combining different sources of information could hence allow drawing robust inference on key habitats in terms of performance, which is of particular interest when including a spatial component in wildlife management and conservation plans and deciding on appropriate habitat improvements. © 2014 The Wildlife Society.

KEY WORDS body mass, Caroux-Espinouse (France), GPS, habitat–performance relationships, habitat quality, home range, Mediterranean mouflon, *Ovis gmelini musimon × Ovis* sp.

Identifying the drivers of population dynamics has long been a central issue in population ecology, wildlife management, and conservation (Caughley 1977, Gaillard et al. 1998). Long-term studies of vertebrates highlighted the complex effects of sex, age, cohort, density, and climate on fitness components and population dynamics of large mammals (Sæther 1997, Gaillard et al. 2000). Because these factors often permitted rather good reconstruction of the past variation of population dynamics (Clutton-Brock and Coulson 2002), the other parameters contrasting life histories of individuals such as acquisition of resources and habitat quality (Van Noordwijk and De Jong 1986) were relatively overlooked until the end of the 20th century. However, identifying the habitat characteristics affecting individual performance is now viewed as a challenging task because ungulate populations, which are often at high density in the northern hemisphere (Côté et al. 2004, Austrheim et al. 2011), face rapid habitat modifications due to global warming and changes in land use that alter resource availability or quality and habitat structure (Loison et al. 2003, Acevedo et al. 2011, Mysterud and Sæther 2011).

By identifying which habitat characteristics best explain inter-individual fitness variability (habitat fitness potential

sensu Wiens 1989), a functional definition of habitat quality could be proposed (Hall et al. 1997, Mosser et al. 2009, Gaillard et al. 2010). Accurate assessments of habitat quality and of the functional relationships between habitat quality and fitness are pivotal for explaining and predicting the temporal dynamics of population distribution under external drivers such as climate and land use changes (Pulliam 1988). Thus, they may constitute a significant contribution to ecological niche analyses and improvement of habitat suitability models (Pulliam 2000, Titeux et al. 2007). Some habitat characteristics were demonstrated to significantly contribute to variation in fitness, most often in interaction with density and climatic variability (e.g., Pettorelli et al. 2003b, 2005; Dugger et al. 2005). However, the habitat characteristics influencing fitness are not only expected to be species-specific but also to differ between and within populations of the same species. Indeed, individuals from different species or populations and within populations have different needs in terms of diets (Tixier and Duncan 1996, Marchand et al. 2013), experience contrasted habitat characteristics, and have different social and anti-predator constraints shaping how they exploit their environment (see, e.g., Nilsen et al. [2004] and McLoughlin et al. [2007] for contrasted results in 2 populations of roe deer [*Capreolus capreolus*]). Therefore, we need to improve our knowledge on habitat–performance relationships at several spatial scales and from individuals to species (Gaillard et al. 2010).

Studies on habitat–performance relationships are still relatively scarce, particularly at the individual scale, one reason being that joint information about fitness and habitat use are difficult to acquire in wild populations of long-lived species (Gaillard et al. 2010). Indeed, estimating survival, reproduction, and habitat use require long-term monitoring of marked individuals and major investments in field work and telemetry equipment. However, in ungulates, body mass has been shown to correlate with variation of most life history traits related to fitness such as reproductive parameters (Hewison and Gaillard 2001, McElligott et al. 2001, Garel et al. 2009b) and juvenile or adult survival (Loison et al. 1999, Côté and Festa-Bianchet 2001). Therefore, studies of factors influencing body mass variation provide relevant insights on major determinants of fitness variation and on their consequences on population dynamics. The importance of landscape structure (Mysterud et al. 2002, Zannèse et al. 2006, Hewison et al. 2009), habitat composition (Coulson et al. 1997), and quality (Mysterud et al. 2002; Pettorelli et al. 2002, 2003a) was for example emphasized for shaping body mass variation between populations or sub-populations of ungulates.

At the individual scale, information on body mass thus could be used in addition to knowledge on individual habitat use, gained in particular from telemetry data (Cagnacci et al. 2010) to connect space use to demographic performance. We propose to achieve this task by combining 2 independent datasets, measures of body mass performed by hunters and information on habitat use derived from Global Positioning System (GPS) monitoring, using data from a population of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.). We hypothesized the home range of harvested individuals to be a circle, whose size and position could be obtained from information on harvest locations and on the distribution of home range sizes determined from the monitoring of GPS-collared rams. We then assessed the contribution of habitat characteristics within hypothesized circular home ranges around a harvest location for explaining inter-individual body mass variation while accounting for the other factors well known to influence body mass such as age, season, and year (Gaillard et al. 2000). As a final evaluation of our approach, we assessed the ability of circles to provide relevant information on the habitat characteristics within home ranges of GPS-collared rams.

Based on previous studies on mouflon diet (Hofmann 1989, Cransac et al. 1997, Marchand et al. 2013), we expected the availability of grass-rich areas to be positively correlated with individual carcass mass (Garel et al. 2007). We also expected a positive correlation between body mass and the local diversity in terms of topography, which could be a proxy for small-scale changes in plant phenology and quality (e.g., Mysterud et al. 2001). Furthermore, steep terrain could have a direct, mechanical negative effect on animal body mass by inducing movement costs (e.g., Lachica et al. 1997). We hence expected habitat and topographic attributes and/or diversity to be related to body mass variation in Mediterranean mouflon rams.

STUDY AREA

We collected data in the Mediterranean mouflon population inhabiting the Caroux-Espinouse massif (43°38′N, 2°58′E, 17,000 ha, 118–1,124 m a.s.l.), at the southern edge of the Massif Central, in southern France (Fig. 1A). In this low mountain region mostly composed of metamorphosed rocks (>90% of the study area), 2 east-west oriented valleys delineate long south or north-facing slopes deeply indented by steep north-south oriented valleys. The main components of mouflon diet in this population (i.e., grasses, but also forbs and shrubs; Cransac et al. 1997) were principally located in open areas covered with moorlands, pastures, meadows, and artificial cultures devoted to wildlife: 59 non-irrigated parcels, mean area ($\pm$SD) = 0.278 $\pm$ 0.217 ha, total area = 16.4 ha, planted with a mix of grasses and cereals (*Festuca* sp., *Dactylis* sp., *Lolium* sp., *Triticum* sp., and *Avena* sp.) by local hunting managers. These areas (hereafter called grass-rich areas) were indeed selected by mouflon as feeding sites (Baudière 1970, Cransac and Hewison 1997). Plateaus (areas with slope $\leq 10°$ and altitude ≥ 900 m a.s.l.; Fig. 1) were largely covered with grass-rich areas (42%) and coniferous trees (35%). The proportion of deciduous trees (beech [*Fagus sylvatica*], chestnut tree [*Castanea sativa*], and holm oak [*Quercus ilex*]) increased with slope (39% on slopes between 10° and 20° vs. 66% on slopes >20°), whereas the ratio of grass-rich to rocky areas in open habitats decreased (84% on slopes between 10° and 20° vs. 49% on slopes >20°; Appendix A). Climatic conditions were at the crossroads of 3 bio-geographic influences: oceanic (in the North and West), Mediterranean (in the South), and mountain influences.
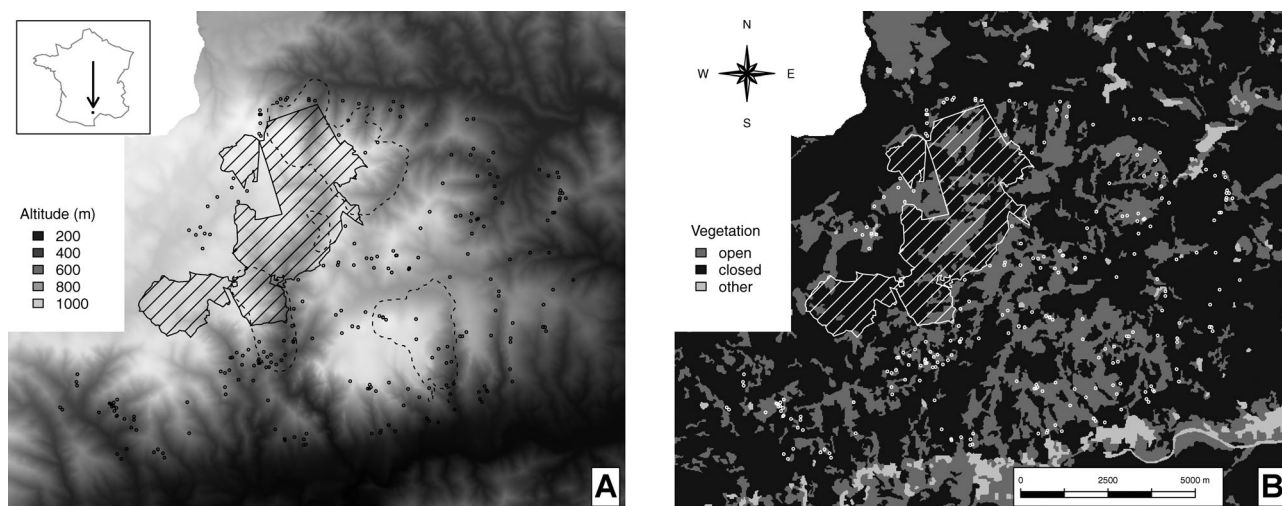
Figure 1. (A) Digital elevation model and (B) vegetation cover (for details on vegetation classification, see Garel et al. 2007) of the range of Mediterranean mouflon population from the Caroux-Espinouse massif (altitude range = 118–1,124 m a.s.l.). The location of the study site in France is given in top left corner. The harvest locations are symbolized by circles. The area shaded with diagonal lines represents the wildlife reserve (1,704 ha). The areas surrounded by dashed lines represent the total range covered by the 95% kernel home ranges of the 13 GPS-collared rams from which data on habitat use allowed us to build hypotheses on home ranges and investigate habitat–body mass relationships in harvested individuals.

The mouflon population has been monitored by the Office National de la Chasse et de la Faune Sauvage since 1974. It originated from 19 individuals (9 males and 10 females) released between 1956 and 1960 in the wildlife reserve situated in the central part of the massif (1,704 ha; Fig. 1). This population currently probably exceeds 2,500 individuals, with the pregnancy rate of adult females reaching 90% (Garel et al. 2005). In the absence of large predators and competitors (wild boar [*Sus scrofa scrofa*] and roe deer were the other ungulate species present in the massif), the population of mouflon has been managed by harvesting based on annual quotas since 1973. Previous studies revealed matching spatial and genetic structures in this population, suggesting the existence of several spatially segregated sub-populations with specific available ranges and limited movements of individuals between them (Maublanc et al. 1994, Martins et al. 2002, Kings and Brooks 2003). Besides, the habitat use of mouflon in this population was relatively stable through the year with restricted seasonal range shifts and no migratory movements (Dubois et al. 1992; see also Results section).

METHODS

Harvest Data
Hunting occurred from the beginning of September to the end of February, except in the wildlife reserve where it was forbidden. Stalking was the most common practice for harvesting males and resulted in a selective harvest of the largest-horned individuals (for details on hunting practices, see Garel et al. [2007]). Assuming that potential biases induced by the selective harvest of males were limited (see Discussion section), we used data collected from 257 adult males from 4 to 12 years old (14 cohorts from 1993 to 2006) stalked during 5 hunting seasons: 2005 and 2007–2010.

Hunters were accompanied by hunting guides who recorded date, age, GPS coordinates, and carcass mass. Carcass mass was measured with a digital hanging scale (±200 g) and was recorded as either full carcass mass (including rumen content; $n = 23$), partially eviscerated carcass mass (with heart, liver, and lungs present; $n = 20$), or eviscerated carcass mass minus bleedable blood ($n = 214$). Because of strong isometric relationships between these 3 measures of carcass mass (Appendix B), we transformed all full and partially eviscerated measures into eviscerated carcass mass, in keeping with previous work on chamois *Rupicapra rupicapra* (Garel et al. 2009*a*). We transformed the harvesting date to Julian date with day 1 beginning on 1 September, the beginning of hunting season. Age was estimated based on counts of horn growth annuli (Geist 1966). Shot animals were stalked during the legal hunting season, according to dates and hunting quotas fixed by the Préfecture de l'Hérault, and tagged with an official reference number in agreement with the French environmental code (Art. R425-2 to 425-13). No additional animals were harvested for the purpose of this study.

Computing Individual Home Ranges
To estimate habitat characteristics that could influence the body mass of harvested individuals, we used information on home ranges provided by the monitoring of 13 GPS-collared adult rams (from 2 to 10 years of age). We captured rams during the springs of 2006–2010 as part of a long-term population monitoring program. We used salt to bait rams into traps in 3 areas representative of the diversity of climatic influences and of habitats found in our study area (see Fig. 1A and Table 1 for details). We treated all animals according to the ethical conditions detailed in the specific accreditations delivered to the Office National de la Chasse et de la Faune Sauvage by the Préfecture de l'Hérault

Table 1. Characteristics of the home ranges of 13 collared rams used to describe the habitat characteristics that a harvested ram encountered. Days refers to the number of days we monitored a collared ram; fixes refers to the number of fixes taken during the same period. We computed fixed-kernel home ranges using an ad hoc method for the smoothing parameter. Divasp is the diversity of 8 aspect classes, slope is the average slope, open is the proportion of open area in a home range, VRM is a vector ruggedness measure, divslope is the diversity of 10°-slope classes. Significant differences between the actual home range composition for each variable and the distribution of the same variable for random home ranges (variable-sized circles centered on animal locations) revealed by randomization tests ($P < 0.05$) are indicated by a "*".

| ID | Age (years) | Days | Fixes | 95% kernel (ha) | 50% kernel (ha) | 95% kernel home range characteristics | | | | |
						divasp	slope (°)	open	VRM	divslope
1100	3	247	2,527	282	66	2.04	22.5	0.326	1.12	1.36
1304	2	427	5,807	286	83	2.03	23.2	0.375	1.20	1.35
1452	>6	281	3,101	308	64	2.05	22.1	0.319	1.08	1.37
1472	6	312	2,728	537	42	1.97	28.4	0.376	1.64	1.15
1541	4	386	4,040	281	71	1.60	20.9	0.624	0.64	1.37
1542	>4	457	5,913	210	38	1.75	20.6	0.451	0.46	1.28
1551	6	428	5,425	299	55	2.06*	22.0	0.266	1.04	1.36
1552	>7	414	5,083	338	66	1.75	18.9	0.511	0.35	1.35
1554	5	435	5,028	285	70	1.68	19.9	0.583	0.67	1.37
1632	5	428	5,865	172	35	1.79	26.2	0.557	1.43	1.25
1814	7	245	1,978	356	81	1.93	28.5	0.321	1.83	1.15
1937	5	324	3,224	387	67	2.04	23.3	0.342	1.20	1.34
974	10	240	2,306	388	67	2.04	24.5	0.382	1.32	1.32

(prefectorial decrees no. 2005-15-057, 2006-15-040, 2008-15-122, 2009-15-059) and the Préfecture de Paris (prefectorial decree no. 2009-014) in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94-1). We fitted rams with Lotek GPS collars 3300S (revision 2; Lotek Engineering Inc., Carp, Ontario, Canada) that were set to record animal locations at intervals of 20 min over 2-day periods (recording period), 1–3 times per month, for about 1 year ($n = 4,079 \pm 1,493$ GPS locations [mean $\pm$ SD]). This monitoring provided information on habitat use of GPS-collared rams (distribution, average size, and seasonal variation of mouflon home ranges; see Fig. 1A, Table 1 and Results for details).

As a first step to defining habitat characteristics possibly encountered by harvested individuals, we used a circle centered on the harvest location and whose size was the average annual home range of GPS-collared rams (computed using fixed 95% kernel with an ad hoc method for smoothing parameter; Table 1 and Fig. 2A). In a second step, we evaluated the robustness of the results gained from this simple approach using a new circular home range whose center was determined on the basis of an azimuth (α_i) and a distance (Δ_i) from the harvest location, and whose size was delineated based on a new radius (r_i). We randomly chose α_i from a uniform distribution between 1° and 360°. We derived Δ_i and r_i from areas (A_{Δ_i} and A_{α_i}, respectively) randomly picked from normal distributions whose parameters were the mean and the variance of the 50% and 95% kernel home ranges of GPS-collared individuals, respectively (Fig. 2B). By following this approach, we were able to delineate home ranges similar in size to GPS-collared individuals and consistent with the intensity of use within individual home ranges corresponding to the probability of harvesting an individual in the highly used area (i.e., the 50% kernel of its home range). We ran this procedure simultaneously for each harvest location and repeated it 1,000 times. We therefore obtained 1,000 potential home ranges for each of the 257 harvested rams.

As a final evaluation, we assessed the ability of circles with variable sizes and center positions to provide reliable estimates of habitat characteristics found within the real home range of GPS-collared animals. Specifically, we compared the observed habitat characteristics within 95% kernel home ranges of GPS-collared individuals with the distribution of simulated habitat characteristics within circles whose radii were derived from areas randomly picked in the distribution of 95% kernel home ranges of GPS-collared individuals (see Table 1) and centered on each animal location (1 circle for each animal location).

Habitat Characteristics

The only vegetation map that encompassed all harvest locations (source: Occupation du sol LR 1999–2006/SIG LR project; www.siglr.org; resolution = 25 m) classified rocky and grass-rich areas into open habitats. However, because of a strong gradient of abundance of grass-rich areas with slope (see Study Area and Appendix A), the proportion of open habitats and mean slope within home ranges together were a proxy of abundance in grass-rich areas within home ranges. We derived mean slope, diversity of slope, diversity of aspect, and mean ruggedness from a digital elevation model (source: BD ALTI ® dataset of the Institut Géographique National; resolution = 25 m). We defined slope in 10° intervals from 0 to $\geq 30°$ and aspect classes as north, northeast, east, southeast, south, southwest, west, and northwest. We computed diversity of slope and aspect using Shannon-Wiener information criteria H' (Hanski 1978; Appendix C). We assessed mean ruggedness within home ranges using the mean vector ruggedness measure (VRM, Sappington et al. 2007; Appendix C). Correlations between covariates were low (<0.43), and not significant ($P > 0.05$).

Statistical Analyses

We first determined a baseline model describing carcass mass variation based on animal age, date of harvest, and cohort effects before investigating the influence of habitat characteristics. We included age in our models as a linear and
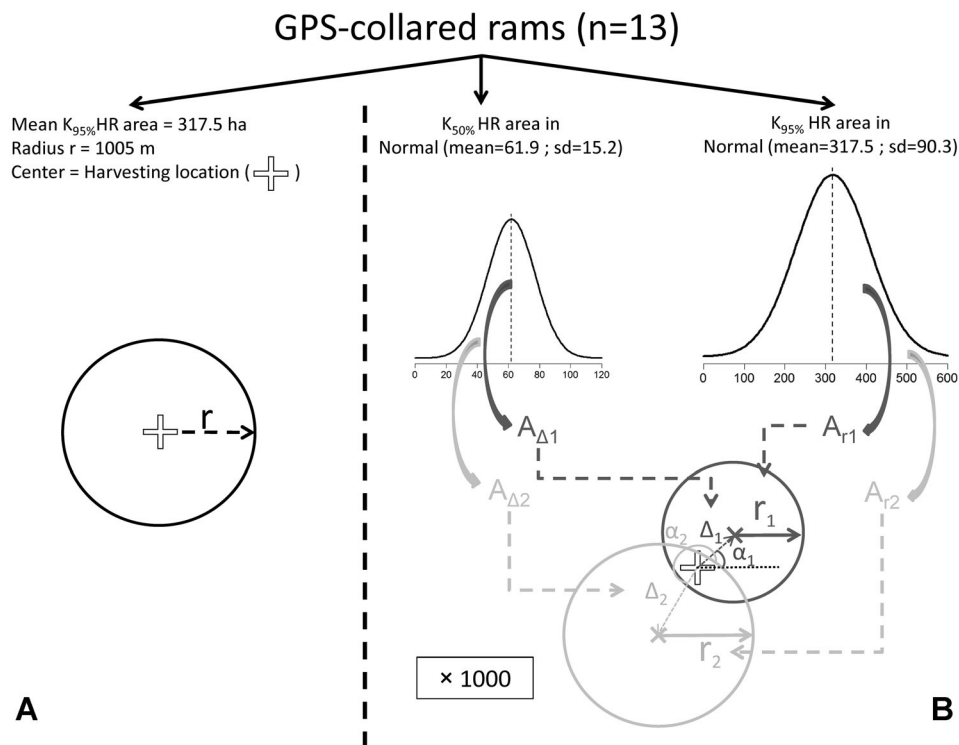
GPS-collared rams (n=13)

Mean $K_{95\%}$HR area = 317.5 ha
Radius r = 1005 m
Center = Harvesting location (✛)

$K_{50\%}$ HR area in
Normal (mean=61.9 ; sd=15.2)

$K_{95\%}$ HR area in
Normal (mean=317.5 ; sd=90.3)

$A_{\Delta 1}$ $A_{\Delta 2}$ A_{r1} A_{r2}

α_2 Δ_1 r_1 α_1

Δ_2 r_2

× 1000

A   **B**

Figure 2. Computational procedure used to determine home range composition of 257 mouflon rams harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France). (A) First, the home range of each harvested ram was hypothesized as being a circle centered on its harvest location with a radius of 1,005 m, corresponding to the average 95% kernel home range area ($K_{95\%}$ HR, 317.5 ha; fixed 95% kernel and ad hoc method for smoothing parameter) of 13 mouflon rams fitted with GPS collars. (B) For each harvested individual, we determined a new circular home range by defining a new center position, based on an azimuth α_i randomly picked in the 360° surrounding the harvest location (α_i follows a uniform distribution) and at a distance Δ_i from the harvest location, and a new radius r_i. We derived Δ_i and r_i from areas A_{Δ_i} and A_{r_i} randomly picked in the normal distributions whose parameters were the mean and the standard deviation of the distributions of the 95% kernel (mean = 317.5 ha, SD = 90.3 ha) and 50% kernel ($K_{50\%}$ HR, mean = 61.9 ha, SD = 15.2 ha) home range areas of the 13 GPS-collared individuals, respectively ($\Delta_i = \sqrt{A_{\Delta_i}/\pi}$ and $r_i = \sqrt{A_{r_i}/\pi}$). The procedure was represented for 2 simulations (dark and light gray, respectively) and for a given harvest location. We ran it simultaneously for each of the 257 rams included in the analysis and repeated it 1,000 times.

quadratic term to account for the leveling off of the increase of body mass with age. We also included date of harvest as a linear and quadratic term because body mass was expected to change throughout the hunting season in conjunction with rutting activities (Mysterud et al. 2004, Garel et al. 2011). Young individuals are the most sensitive age class of the population and conditions encountered during the year of birth generally have long-lasting consequences known as cohort effects (Lindström 1999, Gaillard et al. 2000, Solberg et al. 2004). We accounted for a cohort effect both as a factor and as a continuous covariate (14 different years of birth) because a previous study reported a strong linear decrease in cohort mass over time in this population in response to both selective harvesting and loss of favorable habitats (Garel et al. 2007). We based our model selection on Akaike's Information Criterion with second-order adjustment (AIC$_c$) to correct for small sample bias. When the difference in AIC$_c$ between 2 models was more than 2, we selected the model with the lowest AIC$_c$ (Burnham and Anderson 2002). Among the set of models with ΔAIC$_c$ < 2, we used Akaike weights to compare the relative performance of models in addition to the absolute AIC$_c$ values (Burnham and Anderson 2002). Weights can be interpreted as the probability that a model is the best model, given the data and the set of candidate models.

Once we determined the baseline model, we compared it with the set of potential models including all combinations of the 5 habitat characteristics ($n = 32$). In the simple approach based on fixed-sized circles centered on harvest locations, we determined the relative importance of each variable by summing the Akaike weights across all the models where each variable occurs, the standard errors, and the 95% confidence intervals provided by a model-averaging procedure (Burnham and Anderson 2002; Appendix C). We inspected residuals to detect nonlinear effects and potential interaction among the best covariates (data not shown).

Next, we fitted the set of habitat-based models previously described for each of the 1,000 potential habitat datasets gained from circles with variable size and center position around each harvest location. Because of model selection uncertainty in each of our simulation, we used multi-model inference approaches (Burnham and Anderson 2002, Symonds and Moussalli 2011). To highlight the importance of each habitat variable, we retrieved mean relative importance (mean cumulative relative importance of models including each variable) and relative frequency of occurrence of each variable in AIC$_c$ selected models. Finally, we computed the bootstrap estimators, standard errors (using equations 4.2 and 4.5 from Burnham and Anderson 2002, respectively; Appendix C), and 95% confidence intervals of

each habitat parameters in accordance with model frequencies determined by simulations (Burnham and Anderson 2002).

We assessed the ability of circles with variable sizes and positions around animal locations to provide relevant information on home range characteristics within homes ranges of GPS-collared individuals using randomization tests (Edgington and Onghena 2007). For each GPS-collared individual, we obtained the distribution of the values of each habitat characteristic from the second procedure previously described (variable-sized circles) but with 1 circle centered on each animal location. For each habitat characteristic and each GPS-collared ram, a randomization test allowed us to determine if the observed value within the real 95% kernel home range was in accordance (null hypothesis) or significantly differed (2-sided alternative hypothesis) from the distribution of simulated habitat characteristics within these circles.

We performed all analyses using R version 2.15.1 (R Development Core Team 2013), adehabitatMA and adehabitatHR packages (Calenge 2006) for the computation of habitat variables and of home range composition, respectively, the ade4 package for randomization tests (Dray and Dufour 2007), and the MuMIn package (Barton 2013) for modeling procedures.

RESULTS

We estimated average 95% and 50% annual home range sizes ($\pm$SD) of GPS-collared rams to be 317.5 ± 90.3 ha (range =

171.7–537.2) and 61.9 ± 15.2 ha (range = 34.7–82.8), respectively, and their distributions followed a normal distribution (Shapiro-Wilk normality tests: $W = 0.921$, $P = 0.26$ and $W = 0.894$, $P = 0.11$). Home ranges were rather stable through the year; the mean overlap ($\pm$SD) between seasonal home ranges was $89.8 \pm 2.5\%$ (fixed 95% kernel and ad hoc method for smoothing parameter, with spring = Apr–Jun, summer = Jul–Sep, autumn = Oct–Dec, and winter = Jan–Mar).

The baseline model describing habitat-independent carcass mass variation included age (quadratic term), harvesting date, and cohort as explanatory variables (Table 2). Ram carcass mass increased up to 8–10 years and then leveled off at older ages (Table 3 for model-averaged parameters and Fig. 3A). Carcass mass declined linearly with harvesting date with an average 16.4% (4.3 kg) decline in mass between 2 September and 26 February (Fig. 3B). A model including cohort as a factor had much less support than the model including a linear effect, which indicated a 26.4% (6.9 kg) decline over 14 years (Fig. 3C).

Using circles of fixed size centered on harvest locations, multicollinearity between the habitat covariates was low (variance inflation factors ranged from 1.06 to 1.32). Three habitat characteristics had a high relative importance: the diversity of aspects (0.99), the mean slope (0.79), and the proportion of open areas (0.78, Table 3). Rams with home ranges including a high diversity of aspects had lower carcass mass than rams with homogeneous home ranges (Fig. 4A). Carcass mass decreased by 16.0% (4.1 kg) of the

Table 2. Results for modeling carcass mass of mouflon rams ($n = 257$) harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France) using model selection for a baseline model based on age, harvest date, and cohort without habitat variables and for habitat models added to the selected baseline model. We computed habitat characteristics using fixed-sized individual home ranges centered on harvest locations of rams. K = number of parameters, LL = log-likelihood, w_i = corrected Akaike's Information Criterion (AIC$_c$) weights. Models beginning by a + included the selected baseline model: age + age^2 + date + cohort. Habitat covariates are diversity of aspect classes (divasp), mean slope (slope), proportion of open areas (open), vector ruggedness measure (VRM), and diversity of slope classes (divslope). We present only models with ΔAIC$_c$ < 10 for habitat characteristics.

Models	K	LL	AIC$_c$	ΔAIC$_c$	w_i
Baseline models					
Null	2	−760.8	1,525.6	0	
age + age^2	4	−733.0	1,474.3	0	
age	3	−736.5	1,479.0	4.7	
age + age^2 + date	5	−723.9	1,458.0	0	
age + age^2 + date^2	6	−723.8	1,460.0	2.0	
age + age^2 + date + cohort	6	−716.5	1,445.3	0	
age + age^2 + date + cohort (factor)	18	−711.9	1,462.8	17.5	
Habitat models (all include top baseline model)					
+divasp + slope + open	9	−707.4	1,433.6	0	0.286
+divasp + slope + open + divslope	10	−707.1	1,435.1	1.54	0.134
+divasp + slope + open + VRM	10	−707.2	1,435.3	1.68	0.125
+divasp + slope	8	−709.7	1,435.9	2.29	0.092
+divasp + open	8	−710.1	1,436.7	3.10	0.061
+divasp + slope + open + VRM + divslope	11	−706.8	1,436.7	3.13	0.060
+divasp + open + divslope	9	−709.0	1,436.8	3.19	0.059
+divasp + slope + divslope	9	−709.5	1,437.8	4.15	0.036
+divasp + slope + VRM	9	−709.6	1,437.9	4.31	0.034
+divasp + open + VRM	9	−710.0	1,438.8	5.15	0.022
+divasp + open + VRM + divslope	10	−709.0	1,439.0	5.35	0.020
+divasp	7	−712.3	1,439.1	5.49	0.019
+divasp + slope + VRM + divslope	10	−709.4	1,439.8	6.15	0.013
+divasp + divslope	8	−711.6	1,439.8	6.20	0.013
+divasp + VRM	8	−712.1	1,440.9	7.26	0.008
+divasp + VRM + divslope	9	−711.5	1,441.8	8.18	0.005

Table 3. Parameter estimates for the habitat variables expected to explain variation in body mass of 257 mouflon rams harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France). We obtained estimates, unconditional standard errors, and 95% confidence intervals from model-averaging (fixed-sized circular home ranges with a 1,005-m radius) or from a multi-model inference approach (circular home ranges with variable size and position around harvest locations). We computed habitat characteristics using fixed-sized (1,005-m radius) circular home ranges centered on locations of harvested animals. Habitat covariates are diversity of aspect classes (divasp), mean slope (slope), proportion of open areas (open), vector ruggedness measure (VRM), and diversity of slope classes (divslope).

Variables	Fixed-sized circular home ranges centered on harvest locations				Circular home ranges with variable size and center position around harvest locations		
	Relative importance	β	SE	95% CI	β	SE	95% CI
age		2.30	0.82	0.69; 3.91			
age^2		−0.12	0.05	−0.22; −0.02			
date		−0.02	0.01	−0.03; −0.01			
cohort		−0.53	0.16	−0.83; −0.22			
divasp	0.99	−8.20	2.48	−13.06; −3.34	−4.69	1.55	−7.23; −2.14
slope	0.79	−0.09	0.04	−0.18; −0.01	−0.06	0.02	−0.09; −0.03
open	0.78	3.51	1.66	0.26; 6.76	0.69	0.62	−0.34; 1.73
VRM	0.29	34.30	76.38	−115.41; 184	1.71	2.49	−2.38; 5.80
divslope	0.34	−1.31	1.50	−4.25; 1.63	−0.09	0.10	−0.26; 0.09

average ram carcass mass in our sample between extreme values of aspect diversity. Steep home ranges were also found to be less favorable than flat ones (Fig. 4B) leading to a 9.3% (2.4 kg) decrease in carcass mass when rams experienced extreme values of slope average. Finally, we found home ranges with high proportions of open areas influenced carcass mass of male mouflon positively (Fig. 4C), with carcass mass increasing by 11.4% (2.9 kg) from the least to the most open home ranges. Diversity of slope classes and ruggedness had much less support in our analysis (Tables 2 and 3).

Models using habitat covariates derived from variable-sized circular home ranges provided results similar to those using fixed-sized circles centered on harvest locations. Two models, both including the diversity of aspects and mean slope, and 1 also including the proportion of open areas, were frequently in the set of models with the lowest AIC$_c$ values (Table 4). The probability of 1 of these 2 models being selected was 0.735. Diversity of aspects, mean slope, and proportion of open areas occurred in 87.8%, 84.0%, and 37.9% of the 1,000 selected models, whereas diversity of slope and VRM only occurred in 8.1% and 4.7% of them, respectively. The mean cumulative relative importance of the models in which diversity of aspect, mean slope, and proportion of open areas occurred were 0.767, 0.661, and 0.510, respectively. The negative effects of diversity of aspects and mean slope on carcass mass variation were again strongly supported, as well as the absence of relationships with ruggedness (VRM) and diversity of slopes, whereas the positive effect of open areas was less pronounced (95% CI including 0; Table 3).

Finally, habitat characteristics within the real home range of GPS-collared rams were comparable with the distribution provided by variable-sized circular home ranges centered on animal locations with 1 exception (Table 1). Diversity of aspect for animal ID 1551 significantly differed from the distribution of habitat characteristics in simulated home ranges.
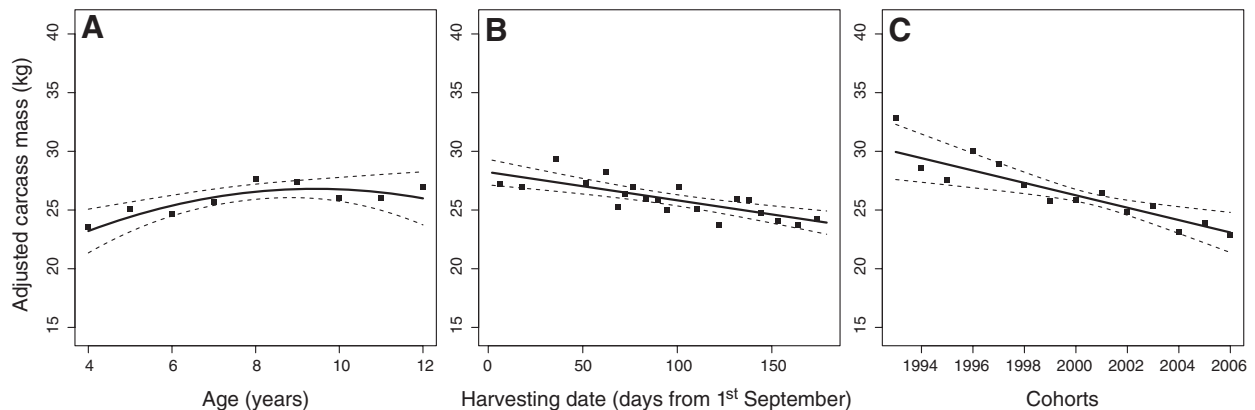

Figure 3. Variation in adjusted carcass mass (kg) of mouflon rams harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France) in response to age (A), harvesting date (days from 1 Sept; B), and cohorts (C). Measures of eviscerated carcass mass are adjusted (hence termed adjusted carcass mass) to control for the other variables included in the model (mean values) and are represented using light gray dots. Solid lines correspond to the linear regressions from the baseline model and dashed lines represent the 95% confidence intervals. Black squares represent the average adjusted carcass mass for the middle of covariable classes (A and C: 1 unit classes; B: 5% quantiles). We computed parameters using fixed home range size and position.
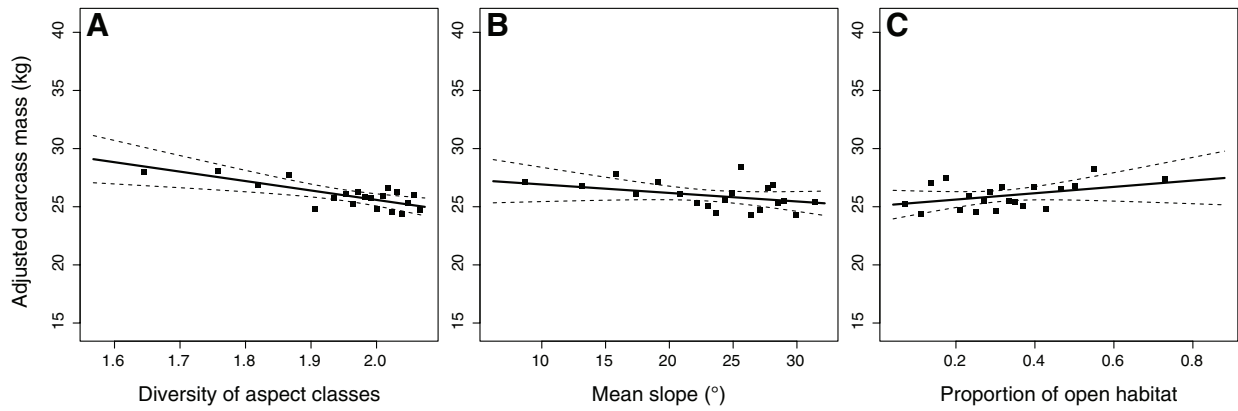
Figure 4. Variation in adjusted carcass mass (kg) of mouflon rams harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France) as a function of diversity of aspect (A), mean slope (B), and proportion of open habitat (C) in their home range (fixed home range size and position). Measures of eviscerated carcass mass are adjusted (hence termed adjusted carcass mass) to control for the other variables included in the model (mean values) and are represented using light gray dots. Solid lines correspond to the linear regressions fitted to the individual data, and dashed lines represent the 95% confidence intervals. Black squares represent the average adjusted carcass mass for the middle of covariable classes (5% quantiles). We computed parameters using fixed home range size and position.

Table 4. Results of linear model selection on habitat characteristics obtained from 1,000 potential home ranges with variable area and position around the culling location of 257 mouflon rams harvested during 2005 and 2007–2010 hunting periods in the Caroux-Espinouse massif (southern France). Models selection probabilities correspond to the number of times each model displayed the lowest corrected Akaike's Information Criterion (AIC_c) value among the 1,000 simulations (Burnham and Anderson 2002). Divasp is the diversity of 8 aspect classes, slope is the average slope, open is the proportion of open area in a home range, VRM is a vector ruggedness measure, divslope is the diversity of 10°-slope classes.

Models	Mean relative importance	Models selection probabilities
+ divasp + slope	0.129	0.455
+ divasp + slope + open	0.121	0.280
+ divasp + slope + divslope	0.058	0.007
+ divasp + slope + open + VRM	0.057	0.015
+ divasp + slope + VRM	0.055	0.010
+ divasp + slope + open + divslope	0.055	0.003
+ divasp	0.054	0.032
+ divasp + open	0.048	0.014
+ divasp + divslope	0.036	0.034
+ divasp + open + divslope	0.034	0.026
+ slope	0.032	0.038
+ slope + open	0.027	0.012
+ divasp + slope + open + VRM + divslope	0.026	0.001
+ divasp + slope + VRM + divslope	0.024	0.000
Baseline model	0.024	0.029
+ divasp + VRM	0.023	0.000
+ open	0.020	0.014
+ divasp + open + VRM	0.019	0.000
+ slope + open + VRM	0.017	0.010
+ slope + VRM	0.017	0.009
+ divasp + VRM + divslope	0.014	0.001
+ divslope	0.014	0.005
+ slope + divslope	0.014	0.000
+ divasp + open + VRM + divslope	0.013	0.000
+ open + divslope	0.013	0.004
+ slope + open + divslope	0.012	0.000
+ VRM	0.009	0.001
+ open + VRM	0.008	0.000
+ slope + open + VRM + divslope	0.008	0.000
+ slope + VRM + divslope	0.007	0.000
+ VRM + divslope	0.006	0.000
+ open + VRM + divslope	0.005	0.000

DISCUSSION

Combining data on carcass mass from hunter-harvested rams and data on home range characteristics gained from GPS-collared individuals, we were able to explore habitat–performance relationships in a long-lived species, Mediterranean mouflon. We found that diversity of aspect classes, mean slope, and proportion of open areas influenced carcass mass in addition to the linear temporal decrease among cohorts previously reported for this population (Garel et al. 2007).

In Norway, aspect diversity was assumed to provide a higher diversity in phenological developmental stages than homogeneous landscapes and to extend the period of access to newly emergent high-quality forage (Mysterud et al. 2001). This may explain the positive influence of topography diversity on body mass of red deer (*Cervus elaphus*), a species for which quality of food is almost as important as quantity (Gebert and Verheyden-Tixier 2001). We found an opposite influence in mouflon rams. This species primarily grazes and relies on the intake of large quantities of slowly digestible food that strongly constrains its daily energy intake, rather than on high quality food (Wilmshurst et al. 1999). Such slowly digestible food may be more limited in areas with a high diversity of aspect. In addition, in our Mediterranean area with its limited altitude range and infrequent, low, and fast-thawing snowfall, a high diversity of aspect may have limited influence on plant phenology and quality compared with Norway.

The influence of mean slope and proportion of open areas within home ranges on ram carcass mass, and the lack of a relationship with ruggedness also suggested that body mass variation in mouflon rams could be mainly influenced by abundance and structure of foraging resources, whereas the direct costs imposed by topography for movements and increased vigilance in rugged habitats (Hayes et al. 1994) could be less predominant. Indeed, open habitats in flat areas and moderate slopes were mainly composed of heather and

broom moorlands, meadows, pastures, and artificial cultures devoted to wildlife, with high proportions of grasses, forbs, and shrubs (i.e., main food resources for mouflon; Baudière 1970, Cransac et al. 1997, Marchand et al. 2013), whereas widespread rocky areas from steep slopes might provide less favorable foraging conditions. In the future, studies relying on the monitoring of numerous animals fitted with GPS collars and detailed information on resource spatial structure and quality should allow us to better explore and firmly conclude on the underlying factors explaining spatial variation in mouflon body mass.

Our approach gave promising results in exploring habitat–performance relationships despite the absence of data on specific habitat use of harvested individuals. The relevance of harvesting data is often questioned because of biases (Martínez et al. 2005) despite their frequent use in ecological and management studies (Solberg and Sæther 1999, Morellet et al. 2007). In our study, hunting intensively occurred in all the habitats where mouflon lived and where hunting was permitted so that all possible habitats in our study area could be reasonably assumed as equally sampled. Because largest-horned (also heavier) rams are preferentially harvested and selection should be easier in open than in forested areas, a stronger selection for heavier rams in open areas could be expected. However, the strong habitat heterogeneity (aspect, slope, and vegetation types) in the study area prevents the existence of correlations between the composition of the entire home range (e.g., proportion of open habitats) and the characteristics of the habitat where mouflon were harvested. Also, GPS data provided the basic knowledge on species home range, such as size, intensity of use, and pattern of seasonal variation, necessary to evaluate the consistency of the results provided by our approach. Simulations on home range sizes and positions allowed us to account for uncertainty on these parameters and their expectable inter-individual variation (McLoughlin and Ferguson 2000, Börger et al. 2006). The analysis of these data confirmed most of the results gained from the approach with fixed-size circular home ranges centered on harvest locations. We also confirmed the ability of circles around animal locations to provide relevant information on habitat characteristics within home ranges of monitored mouflon in our Mediterranean area where restricted seasonal range shifts and no migratory movements have been reported (Dubois et al. 1992). Our approach was hence largely supported in identifying key habitat components in terms of body mass for species or populations with similar characteristics.

MANAGEMENT IMPLICATIONS

Our approach could help improve the management and conservation of numerous species. Indeed, fitness-related parameters are currently collected by wildlife management agencies and private hunting organization (see Gaillard et al. 2010 for a set of fitness indices), and information on individual habitat use (e.g., home range size) can often be found in the literature. Data necessary to implement such analyses are accordingly already available. By allowing managers and conservationists to identify the habitat characteristics explaining spatial variation of these fitness-related parameters, our approach could first help in deciding on the most appropriate habitat improvements. It could also allow managers to define functional units in populations with homogeneous conditions in terms of key habitat characteristics for body mass, decide on the appropriate management within them, and hence integrate the spatial component in management plans. Finally, recording temporal fluctuations of body mass in spatial units previously defined could enable assessment of the equilibrium between populations and their habitats. As such, body mass could thus be used as a spatially explicit indicator of ecological change (sensu Morellet et al. 2007).

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APPENDIX A

We used a second land cover map, covering 60% of the total covered by circles around harvest locations, to give a better description of habitat types in our study area (see Study Area section) and help in the interpretation of our results. We derived this map from the processing (*K*-means unsupervised classification) of a SPOT satellite image taken in July 2005 and field validation (resolution = 25 m; Tronchot 2008). It allowed us, in particular, to distinguish rocky areas (gray) from other open areas (orange) and to distinguish deciduous (light green) from coniferous (dark green) forests. Unfortunately, we could not use it to better distinguish habitat types within circles centered on harvest locations because more than 60% (159/257) of these circles included areas that were not described in this second map (white circles).
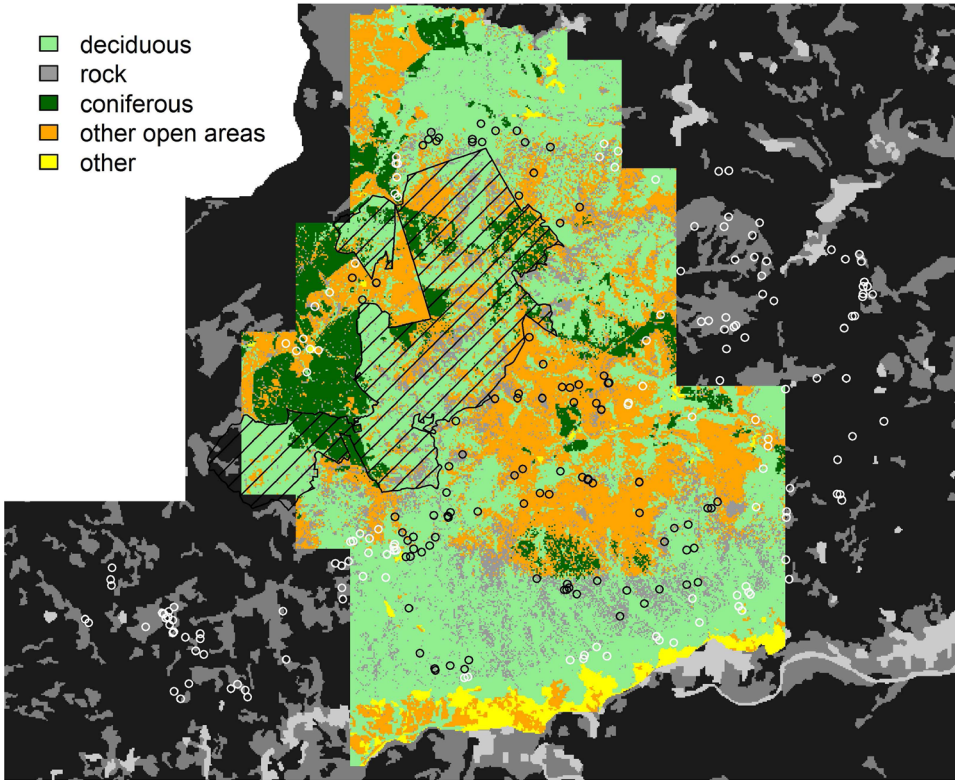
APPENDIX B
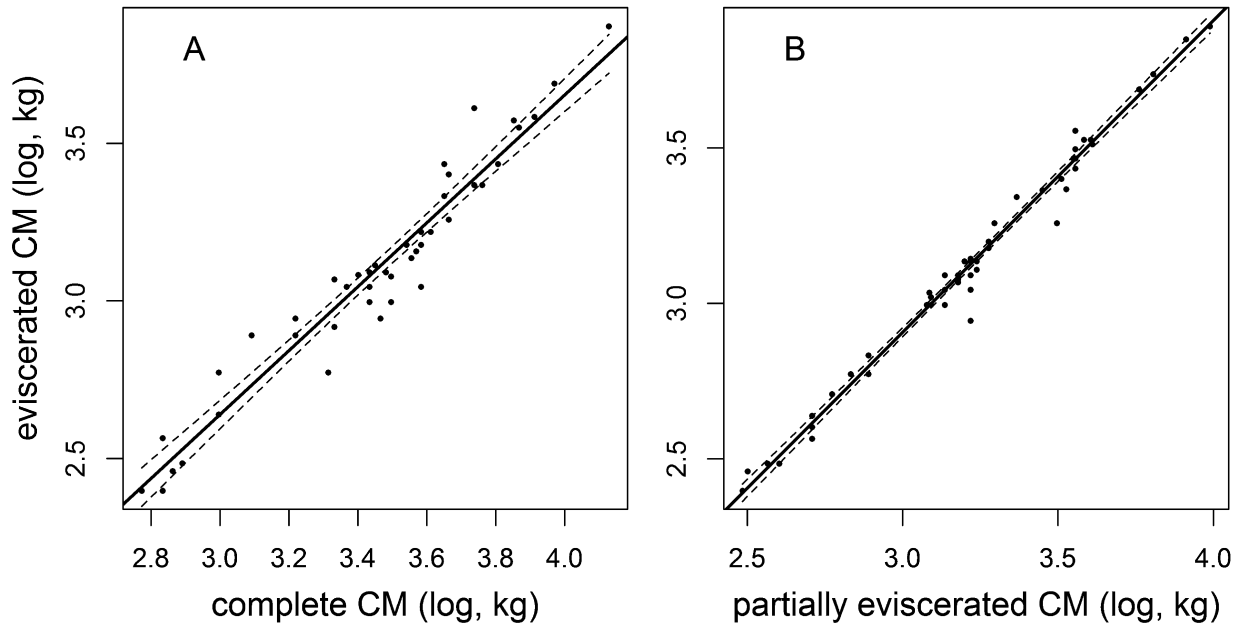
Isometric relationships between eviscerated carcass mass (CM, kg, log-transformed) and (A) complete carcass mass (kg, log-transformed) and (B) partially eviscerated carcass mass (i.e., with heart, liver, and lung, kg, log-transformed) in Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) harvested in the Bauges mountain range (45°40′N, 6°13′E, 350–2,217 m above sea level, A: $n = 45$; B: $n = 55$). Plain and dashed lines represented predictions and 95% confidence intervals from linear regressions (A: intercept = −0.399 [SE = 0.144], slope = 1.013 [SE = 0.042], $r = 0.966$; B: intercept = −0.099 [SE = 0.057], slope = 1.002 [SE = 0.018], $r = 0.992$). We did not find a difference between sex-specific relationships (data not shown).

APPENDIX C. EQUATIONS USED IN THE MANUSCRIPT

Shannon–Wiener Information Criteria *H*′ (Hanski 1978)

$$H' = -\sum_{i=1}^{n}(p_i \ln p_i)$$

where p_i is the proportion of class i and n is the number of classes.

H′ equals 0 when only 1 class is represented in a sample and reaches its maximum when all the classes are present and equally represented.

Vector Ruggedness Measure VRM (Sappington et al. 2007)

$$\mathrm{VRM} = 1 - \frac{\sqrt{\left(\sum_{i=1}^{n} x_i\right)^2 + \left(\sum_{i=1}^{n} y_i\right)^2 + \left(\sum_{i=1}^{n} z_i\right)^2}}{n}$$

where $x = \sin(\alpha) \times \sin(\beta)$, $y = \sin(\alpha) \times \cos(\beta)$, $z = \cos(\alpha)$, $\alpha = $ slope, $\beta = $ aspect, computed with a 3×3 grid cell neighborhood so that $n = 9$ in our case.

VRM ranges from 0 (flat) to 1 (most rugged).

Model Averaged Estimates in Bootstrap Approaches: Equation (4.2) from Burnham and Anderson (2002)

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} \hat{\pi}_i \hat{\theta}_i$$

where $\hat{\bar{\theta}} = $ model averaged parameter estimate, $R = $ number of considered models ($R = 32$ in our case), $\hat{\pi}_i = $ model i selection frequency, $\hat{\theta}_i = $ parameter estimate given model i.

Model Averaged Standard Errors of Parameters in Bootstrap Approaches: Equation (4.5) from Burnham and Anderson (2002)

$$\mathrm{SE}(\hat{\bar{\theta}}) = \sum_{i=1}^{R} \pi_i \sqrt{var(\hat{\theta}_i|g_i) + (\theta_i - \bar{\theta})^2}$$

where $\hat{\bar{\theta}} =$ model averaged parameter estimate, $R =$ number of considered models ($R = 32$ in our case), $\hat{\pi}_i =$ model i selection frequency, $var(\hat{\theta}_i|g_i) + (\theta_i - \bar{\theta})^2 =$ mean square error of $\hat{\theta}_i$ given model i.