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Implications of the forage maturation hypothesis for activity of partially migratory male and female deer

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Abstract. Partial migration is common in a large variety of taxa in seasonally variable environments. Understanding the mechanisms underlying migration is important, as migration affects individual fitness. Migratory herbivores benefit from delayed forage maturation and hence higher food quality during migration and at their summer range, termed the forage maturation hypothesis (FMH). The link between diet quality and rumination time allows migrants eating a higher quality diet to spend less time on rumination, and they can thus allocate more time to additional feeding. However, such an argument implicitly assumes that deer are energy maximizers, while studies have reported also time minimization strategies under risk of predation. Male and female distributions are limited by different factors linked to both body size differences and reproductive strategies, but there is no study investigating differences in activity pattern according to the individual migratory patterns for male and female deer. We here unify the FMH with the hypotheses predicting sex-specific time allocation strategies. To test predictions of sex-specific activity of resident and migratory red deer (*Cervus elaphus*), we analyzed activity data of 286 individuals that were fitted with GPS collars from a population in western Norway. While migrants were more active during the migration itself, we found no differences in activity pattern between migrant and resident deer during the main growth season, neither in terms of proportion of daily time active nor in terms of daily mean movement speed, thus rejecting that deer were energy maximizers. Overall, we found that females were more active during the main growth season even after controlling for body size differences. These patterns are consistent with patterns predicted from sexual segregation theory linked to the reproductive strategy hypothesis. Our study highlights how the understanding of migration can be advanced by considering it in the context of different reproductive strategies of males and females.

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INTRODUCTION

Migration between distinct seasonal ranges is observed in a large variety of taxa including invertebrates, fishes, birds, and mammals (Chapman et al. 2011) and is an especially common phenomenon among ungulates living in seasonal environments (Berger 2004, Bolger et al. 2008).

Individuals tracking better foraging conditions or avoiding predators at a seasonal range may enhance their fitness, and migration is therefore known to have consequences on population structure and dynamics (Fryxell and Sinclair 1988, Mysterud et al. 2001, Chapman et al. 2011). Ungulate migration typically occurs along elevational or latitudinal gradients affecting

onset of plant growth (Albon and Langvatn 1992). Migratory herbivores with summer ranges at higher elevations or latitudes benefit from delayed forage maturation and hence improved food quality over a prolonged time, what is termed the forage maturation hypothesis (FMH; Fryxell and Sinclair 1988, Hebblewhite et al. 2008). Herbivore migration is according to the FMH driven by selection on a phenological gradient of plant development in order to maximize energy intake (Hebblewhite et al. 2008, Bischof et al. 2012). Empirical studies of partial migration, where only a fraction of a population is migratory, have shown that migrants benefit from a higher quality diet relative to resident individuals (Nicholson et al. 1997, Sakuragi et al. 2003, Hebblewhite et al. 2008, Sawyer and Kauffman 2011, Bischof et al. 2012, Gaidet and Lecomte 2013, Merkle et al. 2016).

One of the main reasons for the interest in understanding migration is its link to fitness, and the role of migration as a driver of population processes. A core hypothesis linking ruminant foraging ecology (and thus FMH) to population ecology is the multiplier effect (White 1983), suggesting a mechanistic explanation for why even a slight change in diet quality can affect body growth substantially. There is a close relationship between diet quality and rumination time (Van Soest 1994). By eating high-quality forage, ruminants not only gain more energy per bite, but they also gain due to reduced time required for rumination enabling them to spend even more time foraging (White 1983). In the FMH setting, migrants eating a higher quality diet would then get both more energy per bite and use less time for rumination, which they can subsequently use to feed even more and hence grow more or put on fat. Better body condition of migratory individuals has been argued linked to the multiplier effect (Albon and Langvatn 1992, Mysterud et al. 2001, Gaidet and Lecomte 2013), but there is no study quantifying whether migratory individuals have increased activity levels due to higher quality diet compared to resident individuals within a population. Such an argument implicitly assumes that deer are energy maximizers (Schoener 1971), that is, using the maximum available time for foraging. However, according to foraging theory, individuals could also follow a time minimization strategy, that is, to stop

foraging after obtaining its energy requirement for example to limit risk of predation (Schoener 1971, Hixon 1982).

In polygynous mammals, the sexes have very different constraints on fitness (Clutton-Brock et al. 1982), leading to largely different ecology of males and females (Ruckstuhl and Neuhaus 2005). Both the reproductive strategy and the body size hypotheses, originally framed to explain sexual segregation, predict sex-specific activity patterns, but implicitly with different predictions regarding energy maximization and time minimization. The basis for the body size hypothesis is that the metabolic rate is allometrically related to body mass, while rumen capacity is isometrically related to body mass (Demment and Van Soest 1985). Based on this, the Jarman–Bell principle predicts higher intake of lower quality food and more time spent on rumination with increasing body mass (Demment and Van Soest 1985) and hence lower activity levels for larger herbivores (Mysterud 1998). Larger bodied males are thus predicted to be less active than females from an energy maximization perspective with size-related digestive constraints. Whether this principle applies at an intraspecific level remains debated (Weckerly 2010). The reproductive strategy hypothesis can at first look give seemingly contrasting predictions regarding sex-specific activity pattern. Females with offspring are often found to seek spatial refuges from predators (Bleich et al. 1997), and we would predict time minimization to limit exposure to predators. However, due to the higher energy requirements linked to lactation, reproducing females are generally found to be more active than males (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2002, Prebanić and Ugarković 2015). Both the body size and reproductive strategy hypotheses predict qualitatively females to be more active than males, but the quantitative predictions differ. Only the body size hypothesis predicts sex-specific differences in activity to quantitatively reflect sexual body size dimorphism, that is, no effect of sex on activity after accounting for individual body size.

There is no study investigating differences in activity patterns in herbivores according to the individual migratory tactic for males and females. We here aim to unify the FMH with the theory predicting sex-specific time allocation

strategies. We took advantage of a detailed long-term dataset on a population of red deer (*Cervus elaphus*) in western Norway where more than 400 deer were fitted with GPS collars, of which 286 had activity collars to address this question. Several studies document a higher quality diet of migrants compared to resident individuals at their summer range (Albon and Langvatn 1992, Hebblewhite et al. 2008, Bischof et al. 2012, Merkle et al. 2016). Under an energy maximization strategy, migrant deer are expected to feed more in order to increase their daily energy intake (White 1983). Consequently, their proportion of time active should be higher than resident deer spending more time ruminating, but their daily mean movement speed should be reduced compared to residents since they are expected to spend less time searching for food (P1; Fig. 1). Alternatively, if following a time minimization strategy, migrant deer with higher quality forage are expected to use less time actively feeding if they spend more time in refuge areas (P2; Fig. 1). Differences in forage quality between migrants and residents, as measured based on the normalized difference vegetation index (NDVI; cumulative index of greenness; Bischof et al. 2012), arise largely due to landscape characteristics related to elevation in their summer home ranges (Mysterud et al. 2017). Hence, for energy maximizers, we

predicted an increased proportion of daily time active with increasing home range quality (in our specific case with increasing elevation; Albon and Langvatn 1992, Mysterud et al. 2001) and increasing access to high-quality forage (i.e., cumulative index of greenness; Pettorelli et al. 2005, Hamel et al. 2009, P3; Fig. 1). For time minimizers, we predicted similar or decreased proportion of daily time active with increasing home range quality (P4; Fig. 1). Lastly, the reproductive strategy hypothesis predicts interactions with sex for the above predictions, as males are expected to be energy maximizers, while females are expected to be time minimizers (P5; Fig. 1).

METHODS

Study area

The study area covered the main distribution range of red deer in southern Norway (counties of Hordaland (15,436 km^2), Sogn and Fjordane (18,619 km^2), Møre and Romsdal (15,099 km^2), and Sør-Trøndelag (18,839 km^2; Fig. 2). The area ranges across different landscapes and topography, from coastal flatter areas to high mountains and valleys inland (elevation from 0 to 2405 m a.s.l., highest elevation deer summer range settled around 1,056 m a.s.l), with the fjord landscape in between. A huge altitudinal gradient
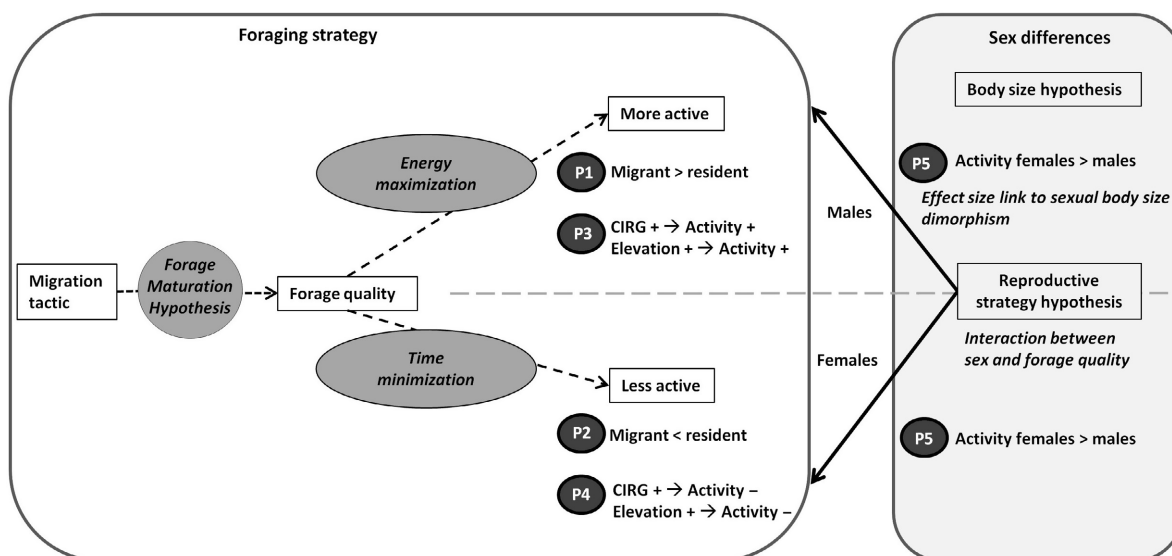
Fig. 1. Schematic representation of the predictions (P1 to P5) and their links within the different contexts/theories and hypotheses. Boxes represent patterns while circles represent processes.
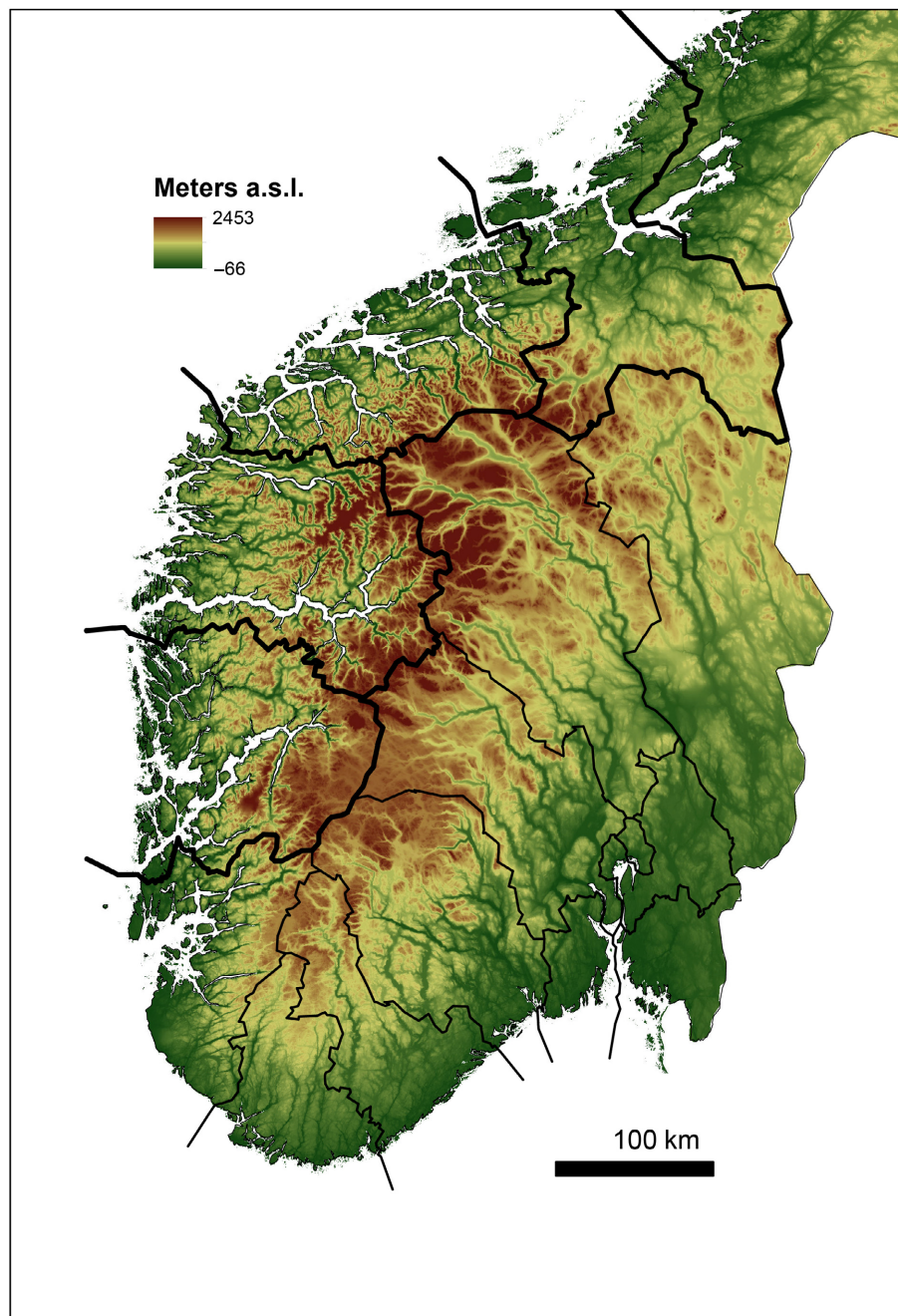
Fig. 2. Map of southern and central Norway showing the gradient of elevation. The four counties of the study area are delineated with thick black lines.

was found in each county (Fig. 2). Vegetation and climate reflect a typical coast–inland gradient, and in general, temperature and precipitation decline from south to north and from coast to inland, while snow depth increases. Forest vegetation is dominated by deciduous species, Scots pine (*Pinus sylvestris*) and planted Norway spruce (*Picea abies*). Agricultural areas are mainly located on flatter ground near the coast or on valley floors. The cultivated fields are mostly

meadows and pastures for grass production. Some grains (*Hordeum vulgare* and *Avena sativa*) are produced in the warmest and most fertile areas, particularly in Sør-Trøndelag county. Red deer population density along the west coast is typically in the range of 1–2 harvested deer per km², roughly equivalent to 5–10 deer per km². Red deer were found to feed on a broad range of species with more than 20 species of graminoids, 30 species of herbs, and five species of shrubs (Albon and Langvatn 1992), and their diet composition mainly includes low shrubs, graminoids, deciduous browse, and herbs (Mysterud 2000). For a more detailed description of the study area, see Mysterud et al. (2011, 2017).

Red deer movement and activity data

Between 2004 and 2015, adult red deer (females ≥1.5 yr; males ≥2.5 yr) were captured mostly during winter (between January and May; mean capture date = 7 March ± 23 d) and fitted with GPS collars (model Tellus 2D; Televilt/Followit, Stockholm, Sweden and model GPS Pro Lite 3; Vectronic, Berlin, Germany) scheduled to take a GPS position every hour or every second hour. Animals were darted and immobilized at feeding sites or on cultivated fields along roads in wintering grounds. During capture, we recorded body weight on most animals (body mass range for males: 70–205 kg, females: 59–153 kg) and all deer were individually tagged. All capture and marking procedures have been approved by the Norwegian Animal Research Authority, and chemical immobilization and marking follow standard protocols (Sente et al. 2014). Some collars included a dual-axis acceleration sensor that counts the individual neck movements in both horizontal and vertical directions (Löttker et al. 2009, Heurich et al. 2012, 2014). Data on movement, based on GPS location only, were available for 412 individuals, while data from activity sensors were available for 286 individuals. Data from the first 24 h after marking were discarded, and the raw data were screened for outliers (Bjørneraas et al. 2010). Only individuals with data spanning between capture to 1 August were included in the analyses. Individual space use tactic (migrant or resident) was determined using the net-square displacement technique (Bunnefeld et al. 2011) adapted by Mysterud et al. (2011) so that individual fit was assessed manually, as in our

previous work (Bischof et al. 2012). From the sensor included in the Vectronic collars (56 out of the 216 individuals), activity data were measured every 8th second and average every 5-min intervals (mean ± SD daily activity counts provided by the collar = 31.62 ± 37.35; activity sensor values range from 0 to 255), while from the Televilt/Followit collars (160 out of the 216 individuals), activity data were provided together with the GPS location at a rate of one data point every hour or two hours (mean ± SD daily activity counts provided by the collar = 5.20 ± 7.83; activity sensor values range from 0 to 215). Each activity value was set as either active or inactive. Because activity sensors were sensitive to any neck movement including head shaking (Löttker et al. 2009, Heurich et al. 2014), all the counts lower than 25 for the Vectronic collars and lower than 3 for the Televilt/Followit collars were set as inactive (see Appendix S1). These thresholds were based on previous studies conducted on red deer with Vectronic collars or ETHOSYS activity counters (Pepin et al. 2006, Löttker et al. 2009). Since activity data were not gathered at the same temporal scale for both collar brands, we used the proportion of daily time active as a metric of activity. The proportion of daily time active was calculated as the number of activity values set as active during a day divided by the total number of activity values obtained from that day. We calculated the movement speed between locations (in m/h) as the distance between two consecutive GPS locations divided by the time between these locations. The daily mean movement speed was then calculated as the mean of the speed between consecutive locations of each Julian day. Any days with less than five activity values or GPS locations were discarded.

Landscape features

Seasonal (i.e., winter and summer) home ranges were estimated using the 95% fixed kernel density estimator with an ad hoc method used for the smoothing parameter in the R package "adehabitatHR" (Calenge 2006). Winter and summer are hereafter referred to seasonal ranges, while spring and fall are referred to as seasonal migration events. For migrant deer, individual migration events were used to define the seasonal home range period. For resident deer, GPS locations between the median spring migration

arrival date (among migrants; 11 May) to the median fall migration departure date (10 September) were used to define the summer range, and GPS locations between the median fall migration arrival date (16 September) to the median spring migration departure date (1 May) were used to define the winter range. Different digital maps providing landscape details on distance to coastline (in km), elevation (m a.s.l.), slope (degrees; 0–90), aspect (degrees; 0–360, where 0 is north and 180 is south), proportion of habitat types (pasture, forest, mountain and other) were used to extract these features at the home range scale. All maps were rasterized with a resolution of 100×100 m. The normalized difference vegetation index, a known proxy of forage quantity and quality for ungulates (Pettorelli et al. 2005, Hamel et al. 2009), was used to estimate the amount of high-quality forage each individual had access to over the entire growth season (1 April–31 August). For each day, we extracted the instantaneous rate of green-up (IRG), derived from the NDVI (see Bischof et al. 2012 for details), for the individual pixels visited by red deer. The IRG is a value between 0 and 1, where 1 represents the peak green-up, that is, when the forage has the optimal balance between quality and quantity. The daily IRG values experienced by an individual were summarized over the growth season (cumulative instantaneous rate of green-up; CIRG), representing its total access to high-quality forage (Bischof et al. 2012). Data on landscape covariates were available from previous works (see Bischof et al. 2012) as means within seasonal ranges and were updated when needed. Elevation, calculated as the mean elevation of all GPS locations at the corresponding seasonal range, was correlated with most of the landscape features (Pearson's product–moment correlation with elevation: correlation = 0.51 with slope, 0.41 with % other, 0.31 with % pasture, 0.31 with % mountain, 0.09 with aspect, 0.05 with home range size, and 0.04 with CIRG; Appendix S2), so based on a conservative threshold of $r = 0.3$ (Zuur et al. 2009), only home range size, aspect, and CIRG were further considered, together with elevation.

Data analysis

During their migration movement, migratory individuals were more active and moved faster than residents during the same period and also compared to before or after the migration event (see Appendix S3 for details). To avoid any bias linked to the specific behavior of migratory deer during their migration, we removed data from days during the migration event (mean spring migration duration = 9.2 ± 12.3 d; mean fall migration duration = 6.5 ± 12.7). Further, some individuals were removed due to missing values in the covariates (i.e., 70 from the dataset on activity and 83 from the dataset on movement); 216 individuals were available for analyses on proportion of time active (N_{count} = 18,892 total daily count) and 329 on daily mean movement speed (N_{count} = 45,308 total daily count).

Model structure.—To answer our question on activity levels according to migration status, we investigated activity and movement patterns using generalized additive mixed models implemented in the R package "mgcv" (Wood 2011). Specifically, we modeled the proportion of daily time active and the daily mean movement speed according to the individual migration status (migrant vs. resident), the Julian date (with a spline effect allowing for non-linear relationships), CIRG, home range size, elevation, and aspect of the home range. The distance of the winter home range barycenter to coastline was included as a fixed effect to account for location differences in the study area. Because patterns were expected to be sex-specific, two-way interactions with sex were considered for migration status, Julian date, CIRG, home range size, elevation, and aspect. Individual identity and year were included as random effects in all models to account for unbalanced sample size. Since the type of activity data differed according to the collar brand, this factor was included in the models explaining the proportion of daily time active. In a similar way, the base scheduled GPS program (every one or two hours) was included in the models explaining the daily mean movement speed. Because elevation and distance of the winter home range barycenter to coastline were highly correlated (Pearson's product–moment correlation: correlation = 0.58, $n = 647$, $t = 17.96$, df = 645, $P < 0.001$), these factors were not included in the same model to avoid correlation issues (Appendix S2). All variables were rescaled and/or transformed when necessary to optimize estimation (Zuur et al. 2009), more specifically, the proportion of daily time active was transformed using an arcsin (x^*2/π) function

allowing the results to be rescaled between 0 and 1, and the daily mean movement speed was log-transformed (see Appendix S4 for distributions).

Model selection approach.—We fitted the global models described above as well as all simpler derived models in R using the AICcmodavg package (Mazerolle 2015). The best models were then selected using the Akaike information criterion corrected for small sample size (AIC$_c$), which reflects the best compromise between model precision and accuracy (Burnham and Anderson 2002, Symonds and Moussalli 2011). According to the rule of parsimony, we selected the simplest model within two AICc of the top model (Burnham and Anderson 2002). We also calculated AICc weights (AICcW) as a measure of the likelihood that a given model was the best among the set of fitted models. Using the sum of the AICcW (termed the predictor weight), we estimated the relative importance of each variable and interactions according to (Symonds and Moussalli 2011). The predictor weight can be interpreted as being equivalent to the probability that the predictor is a component of the best model.

Body mass effect.—Because the differences observed between the sexes can partly be due to differences in body size, with bigger individuals expected to show lower levels of activity (Ruckstuhl 1998), we conducted an additional analysis including body mass as a covariate using the subsample of individuals with known body mass (N_{ind} = 239 and N_{count} = 32,532 for activity data, N_{ind} = 279 and N_{count} = 38,386 for movement). The same model selection procedure was used with the full model including all the covariates selected from the first analysis in addition to the body mass and sex interaction. Since capture dates varied and body mass decreased through the winter (slope = −0.0009 log[kg] per day, SE = 0.0003, P = 0.008), we standardized recorded body mass at capture to the median capture date (8 March). If difference in body size was driving the difference in pattern observed between sexes, then we would expect models including body mass to perform better than model including sex. All analyses were run in R version 3.2.5 (R Development Core Team 2016).

RESULTS

From the 330 red deer captured and with known migration status, 55.1% were migratory, with a higher proportion of migratory males compared to females (50.8% in females and 67.4% in males). The mean distance between the seasonal ranges was 20.4 ± 17.5 km (Table 1). All four counties showed similar proportions of migratory deer in their populations (Hordaland: 51.8 ± 5.4%, Sogn and Fjordane: 57.6 ± 5.4%, Møre and Romsdal: 52.9 ± 4.5%, and Sør-Trøndelag: 63.4 ± 7.5%).

The best model explaining the proportion of daily time active included the two-way interactions of seasonal home range size, home range elevation, and Julian date with sex, as well as the effect of collar brand (Table 2; Appendix S5). The individual migration status and forage quality measured by CIRG were not included in the top-ranked models (P2, P4; Table 2); hence, we could reject predictions from the energy maximization strategy (P1, P3). The proportion of daily time active was higher for females (P5) and varied according to Julian date, starting with an increase for both sexes but then the pattern differed for males and females throughout the summer (Table 3a, Fig. 3a). The proportion of daily time active decreased as the home range elevation increased (P4), especially in females (P5; Table 3a, Fig. 3b), and it increased as home range size increased, but only for males (Table 3a, Fig. 3c).

Table 1. Descriptive features of seasonal home ranges according to the individual sex and migration status category.

Status	Winter home range size (ha)	Summer home range size (ha)	Seasonal range altitudinal difference (m)	Distance between seasonal ranges (km)
Migrant females	1254.5 ± 2473.7	950.5 ± 2336.6	206.3 ± 184.4	17.9 ± 14.7
Resident females	561.1 ± 464.4	496.7 ± 564.5	93.2 ± 157.7	1.0 ± 0.9
Migrant males	3348.5 ± 7891.8	1273.7 ± 1465.6	226.2 ± 233.2	24.7 ± 22.4
Resident males	2453.7 ± 3372.4	923.2 ± 839.2	82.6 ± 169.3	1.3 ± 1.1

Table 2. Predictor weights calculated as the sum of the Akaike weights for each model in which that variable appeared in the complete model selection performed.

Covariate (fixed effect)	Proportion of daily time active (N = 216)[a]	Daily mean movement speed (N = 329)[a]	Proportion of daily time active (N = 239)[b]	Daily mean movement speed (N = 279)[b]
Julian Day (non-linear, interaction with sex)	**1**	**1**	–	–
Julian Day (non-linear)	–	–	**1**	**1**
Sex	**1**	**1**	**1**	**1**
Migration status	0.46	0.38	–	–
Home range elevation	**1**	**1**	**1**	1
Home range size	**0.98**	**1**	**1**	1
Home range aspect	0.36	0.47	–	–
Cumulative instantaneous rate of green-up (CIRG)	0.5	**0.83**	–	0.66
Winter home range distance to coastline	0.01	0.01	–	–
Collar brand	**1**	–	**1**	–
GPS schedule program	–	0.73	–	–
Migration: sex	0.17	0.14	–	–
Home range elevation: sex	**0.96**	**1**	–	–
Home range size: sex	**0.73**	**1**	–	–
Home range aspect: sex	0.11	0.26	–	–
CIRG: sex	0.14	**0.60**	–	–
Body mass	–	–	0.34	**0.94**
Body mass: sex	–	–	0.10	**0.83**

Notes: Analyses were performed with proportion of daily time active or daily mean movement speed as a response variable and (a) without and (b) with the fixed effect of individual body mass. Variables retained in the selected model are in bold. Deer identity and year were included as random factors in all models. Dashes denote that the corresponding factor was not included in the full model.

The best model explaining the daily mean movement speed included the two-way interactions of seasonal home range size, home range elevation, CIRG, and Julian date with sex (Table 2; Appendix S5). The individual migration status was not included in the top-ranked models (P2, contradicting P1; Table 2). As for the proportion of daily time active, the daily mean movement speed showed a similar pattern with higher speed recorded for females that varied according to Julian date, with a different pattern for males and females (P5; Table 3a, Fig. 4a). The daily mean movement speed decreased as the home range elevation increased (P4), especially in males (Table 3a, Fig. 4b), and it also increased as home range size increased, but only for females (Table 3a, Fig. 4c). Finally, daily mean movement speed increased as CIRG increased for females while it decreased for males (Table 3a, Fig. 4d).

Body mass was not included in the best model explaining the proportion of daily time active when adding it as a covariate (Table 2; Appendix S5). However, the addition of the two-way interaction between body mass and sex led to a better fit for the model explaining the daily mean movement speed (Appendix S5). Indeed, daily mean movement speed decreased sharply as body mass increased in males while there was no such relationship for females (Table 3b, Fig. 5).

DISCUSSION

Understanding the mechanisms for how migration may increase individual performance is crucial, as it links individual level foraging to population-level dynamical processes. Based on foraging theory of ruminants, we would expect increased dietary quality to lead both to more energy per bite, but also that less time for rumination leads to even more time spent active foraging. Previous studies on the same population have shown that migrant deer followed the sequential flush of newly emergent high-quality forage during their migration (Bischof et al. 2012, Mysterud et al. 2017). Surprisingly, despite their access to a higher diet quality (Bischof et al. 2012, Mysterud et al. 2017), migrant deer did not allocate more time to activity compared to residents (P2, contradicting P1). Indirectly, our results thus give no support to the notion that

Table 3. Parameter estimates, associated standard error (SE), *t*-value and *P*-value of the selected generalized additive mixed models explaining variation in proportion of daily time active or daily mean movement speed during the main growth season; (a) without and (b) with the fixed effect of individual body mass. Deer identity and year were included as random factors in all models.

Response variable	Model variable (fixed effect)	Estimate	SE	*t*-value	*P*-value
(a) With fixed effect of individual body mass					
Proportion of daily time active (N = 216)†	Intercept	0.29	0.004	66.30	<0.001
	Collar (Vectronic)	0.04	0.007	5.57	<0.001
	Spline (Julian date by sex) (Male)	0.08	0.014	5.38	<0.001
	Spline (Julian date by sex) (Female)	0.04	0.011	3.34	<0.001
	Sex (Male)	−0.03	0.007	−4.81	<0.001
	Home range elevation	−0.01	0.002	−7.00	<0.001
	Home range size	−0.0006	0.001	0.56	0.577
	Home range elevation: sex (Male)	0.008	0.002	2.79	0.005
	Home range size: sex (Male)	0.003	0.002	2.03	0.042
Daily mean movement speed (N = 329)‡	Intercept	4.50	0.042	107.02	<0.001
	Spline (Julian date by sex) (Male)	0.41	0.070	5.78	<0.001
	Spline (Julian date by sex) (Female)	0.41	0.054	7.60	<0.001
	Sex (Male)	−0.15	0.088	−1.68	0.094
	Home range elevation	−0.10	0.008	−12.51	<0.001
	Home range size	0.11	0.005	20.18	<0.001
	Cumulative instantaneous rate of green-up (CIRG)	0.003	0.001	2.45	0.014
	Home range elevation: sex (Male)	−0.05	0.013	−3.84	<0.001
	Home range size: sex (Male)	−0.11	0.009	−11.83	<0.001
	CIRG: sex (Male)	−0.005	0.002	−2.08	0.038
(b) Without fixed effect of individual body mass					
Proportion of daily time active (N = 239)§	Intercept	0.30	0.004	77.09	<0.001
	Collar (Vectronic)	0.03	0.006	5.79	<0.001
	Spline (Julian date)	0.05	0.008	6.52	<0.001
	Sex (Male)	−0.04	0.006	−6.12	<0.001
	Home range elevation	−0.007	0.001	−6.01	<0.001
	Home range size	0.003	0.0006	4.53	<0.001
Daily mean movement speed (N = 279)¶	Intercept	4.45	0.73	6.07	<0.001
	Spline (Julian date)	0.42	0.051	8.28	<0.001
	Sex (Male)	2.44	1.15	2.12	0.034
	Body mass	0.03	0.16	0.17	0.866
	Home range elevation	−0.14	0.007	−19.08	<0.001
	Home range size	0.06	0.005	12.77	<0.001
	Body mass: sex (Male)	−0.58	0.24	−2.41	0.016

† Random effect standard deviation: deer identity = 0.03; year = 0.03.
‡ Random effect standard deviation: deer identity = 0.20; year = 0.16.
§ Random effect standard deviation: deer identity = 0.04; year = 0.02.
¶ Random effect standard deviation: deer identity = 0.19; year = 0.19.

deer are strict energy maximizers (contradicting P1 and P3) but rather have an element of a time minimization (P2 and P4) foraging strategy (Fig. 1). Further, we found that females were more active than males during the main growth season even after controlling for body size differences (P5), suggesting higher energy demands of reproducing females forcing them to forage more as predicted from the reproductive strategy hypothesis (Ruckstuhl and Neuhaus 2002).

Forage maturation hypothesis—Time minimization or energy maximization?

The forage maturation hypothesis predicts that herbivores should follow a phenological gradient of plant development in order to maximize energy intake (Hebblewhite et al. 2008, Bischof et al. 2012), and that migrants obtain a higher quality diet compared to resident is strong evidence in favor of FMH. However, our study does not support the prediction of increased activity
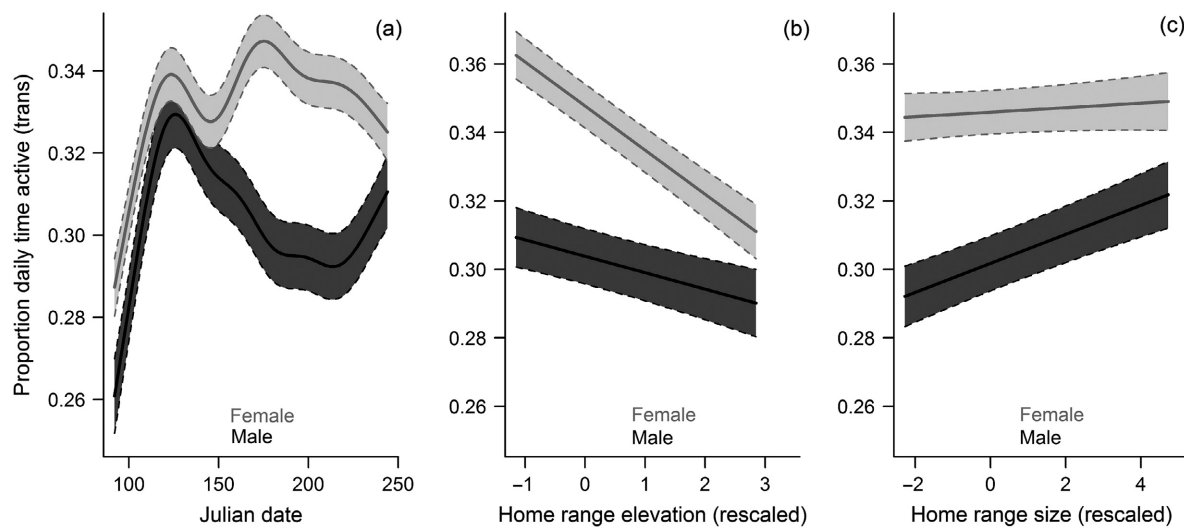
Fig. 3. Relationships between the proportion of daily time active and (a) Julian date, (b) home range elevation, or (c) home range size for both sexes. Julian date, home range size, and elevation are set to their mean values if not shown on the *x*-axis. Individual identity and year are included as random factors (N_{ind} = 216; N_{count} = 18892). The solid and dashed lines depict relationships predicted by the selected models and their 95% confidence intervals, respectively. Note that for clarity, only results from Vectronic collars are shown.

with enhanced forage quality, as activity patterns were (1) similar among migrants and residents during the main growth season and (2) not linked to forage quality as measured by the CIRG. Our results suggest that red deer do not follow pure energy maximization principles. However, results are not fully consistent with pure time minimization either, as access to higher quality forage should then lead to reduced activity time if individuals spend more time at rest. The only result supporting this was a decrease in activity levels as elevation increased. Since body weight in red deer is positively related to a variable topography (diversity of altitude and aspect; Mysterud et al. 2001), an increase in elevation is linked to an increase in the nutritional quality within the home range (note that in our study, within home range elevation was correlated with within home range variation in elevation; Mysterud et al. 2017). The individual foraging behavior can be difficult to determine along the time minimization and energy maximization continuum, both in general and for our data, as all activity is not necessarily foraging. However, as our observation period is outside of the rutting season and the migratory period, it is a fair assumption that activity is mainly linked to movement connected

with foraging activity. In an attempt to classify ungulates, species differing in their body size and digestive ability (African buffalo, *Syncerus caffer*; plains zebra, *Equus quagga*; sable antelope, *Hippotragus niger*) as either energy maximizer or timing minimizer (Owen-Smith and Goodall 2014), failed to validate any of the foraging strategy based on their daily activity patterns. However, studies on bison (*Bison bison*) reveal that rules of energy intake maximization were not sufficient to explain individual foraging behavior (Fortin et al. 2003, Merkle et al. 2015) and that bison rather behave as time minimizers (Bergman et al. 2001). Lastly, the framework focusing solely on energy and time has been criticized for not being nutritionally explicit and unidimensional (Raubenheimer et al. 2009). The foraging strategy used by individuals can be more complex; for instance, brown bears (*Ursus arctos*) are optimizing their dietary protein diet from different sources rather than maximizing the net energy intake, consequently maximizing their mass gain (Robbins et al. 2007). Therefore, the details behind migratory behavior, activity patterns, and individual growth may be complex, and further integration with other ecological theories may advance our understanding further.
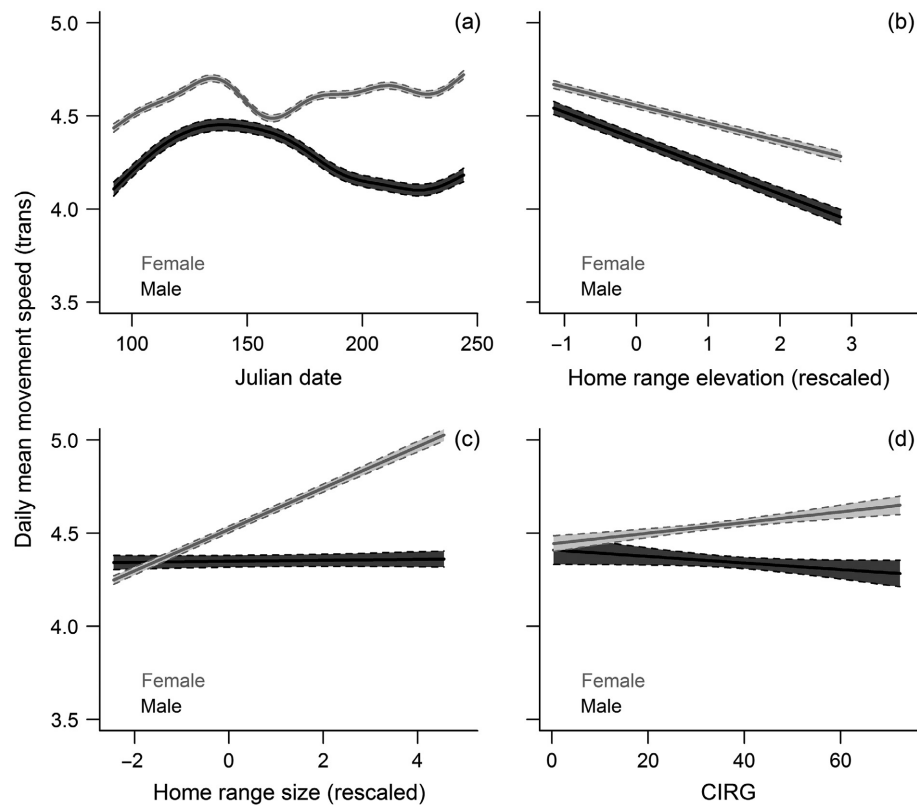
Fig. 4. Relationships between daily mean movement speed and (a) Julian date, (b) home range size, (c) home range elevation, or (d) cumulative instantaneous rate of green-up (CIRG) for both sexes. Julian date, home range size, elevation, and CIRG are set to their mean values if not shown on the *x*-axis. Individual identity and year are included as random factors (N_{ind} = 329; N_{count} = 45,308). The solid and dashed lines depict relationships predicted by the selected models and their 95% confidence intervals, respectively.

Sex differences in ecology and activity

Ultimately, sexual differences in ecology including activity patterns are the evolutionary response to differences in reproductive strategy of male and females in ungulates. Different activity budgets between the sexes are widespread and also an important mechanism to explain social segregation (Conradt 1998, Ruckstuhl 1998). This is termed the activity budget hypothesis, and it has been supported in several species (Conradt 1998, Ruckstuhl 1998, Ruckstuhl and Neuhaus 2002, Bonenfant et al. 2004, Calhim et al. 2006, but see MacFarlane and Coulson 2007, Pérez-Barbería et al. 2007). For example, bighorn sheep (*Ovis canadensis*) females were found to spend more time feeding and were walking more than males (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2002). In red deer, females are earlier reported to

be more active than males regardless of season (Kamler et al. 2007, Prebanić and Ugarković 2015). Similarly, we found higher activity levels in terms of both proportion of daily time active and daily mean movement speed for females compared to males, irrespective of their migration pattern. Such differences in activity between the sexes might be due to differences in body size, since activity time has been found to decrease allometrically with increasing body weight in temperate ruminants (Demment and Van Soest 1985, Mysterud 1998). However, even after accounting for body size differences, we found that females still showed higher activity levels than males. However, a decrease in movement speed was found with increasing body mass only in males, suggesting that males' and females' activity budgets are limited by different factors.
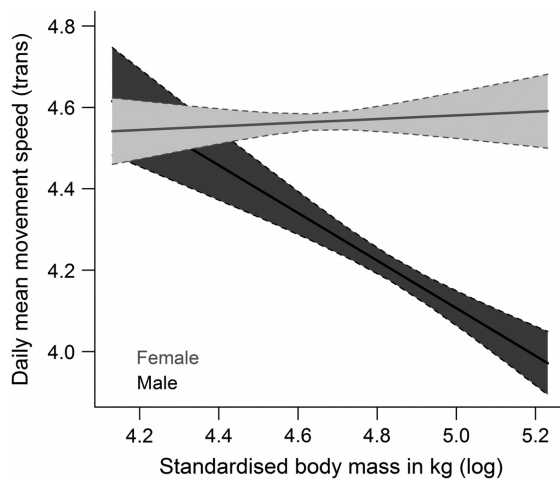
Fig. 5. Relationships between daily mean movement speed and individual body mass, for both sexes. Julian date, home range size, and elevation are set to their mean values and individual identity and year are included as random factors (N_{ind} = 279; N_{count} = 38,386). The solid and dashed lines depict relationships predicted by the selected models and their 95% confidence intervals, respectively.

Trade-offs between foraging demands and avoiding predation risk often affect time allocation patterns (Lima and Bednekoff 1999), and changes in activity levels related to predation risk are commonly observed in a range of organisms (Strobbe et al. 2011, Ross et al. 2013, Koivisto et al. 2016). Ungulate females with offspring are at higher risk, but at the same time limited by their higher energy requirements linked to lactation. Different habitat selection of males and females in our study population is consistent with predation risk avoidance (Bonenfant et al. 2004). Females may thus seek refuges to ensure the protection of their offspring at heel, while males mainly forage to grow and gain fat for the upcoming rutting season, therefore being more willing to expose themselves. The constraints directly or indirectly linked to reproduction can then differ strongly between the sexes during the growth season.

As expected and previously reported for red deer, activity patterns varied throughout the summer season (Berger et al. 2002, Pepin et al. 2006), and activity increased as home range size increased (Allen et al. 2014, Morelle et al. 2015).

Although females were always more active than males, the magnitude of the difference varied throughout the growth season and as home range quality increased. When summer home range elevation increased, females decreased their proportion of daily time active more than males, but less their daily mean movement speed. This is consistent with females being more toward time minimizers and males being more toward energy maximizers. When the CIRG increased (meaning more access to good quality food for a longer period through the growing season), female daily movement increased but male daily movement decreased (Fig. 4d); hence, at high value of CIRG (highest home range quality), the difference in daily mean movement speed between males and females was highest. A decrease in sex differentiation following a reduction of resources is consistent with other studies (Bonduriansky 2007, Mänd et al. 2013). Landscape structure (e.g., habitat composition, topography, fragmentation) within the home range and human disturbance may also influence individual activity patterns; for example, how foraging areas are scattered within the home ranges may directly influence their movement patterns. Further investigations at smaller scales would be necessary to gain insight on how fine-scale landscape structure and human disturbance influence activity patterns in both sexes. Indeed, Allen et al. (2014) reported how female red deer movement and feeding patterns were influenced by landscape composition and fragmentation in Sweden, highlighting the importance of the trade-off between forage and cover. Deer browsing impacts the forest, leading to conflicts with the forestry industry (Gerhardt et al. 2013). In turn, forestry practices influence deer movement and activity and hence level and distribution of browsing damages. Borkowski and Ukalska (2008) found that introduction of forest understories into mature pine forests led to higher use by red and roe deer that were attracted by a combination of both food and cover and should then promote big game management. Better knowledge of deer behavior is thus of particular interest to improve both forestry practices and sustainable deer populations to minimize conflicts between different stakeholders (Borkowski and Ukalska 2008, Jarnemo et al. 2014).

Conclusion

With the rise of GPS collars and satellite-derived measures of plant phenology (NDVI), there is a considerable progress toward measuring more in detail how well migratory herbivores follow the green wave as predicted from the FMH (Sawyer and Kauffman 2011, Bischof et al. 2012, Merkle et al. 2016, Rivrud et al. 2016). It is also documented that resident and migrant individuals may experience different trade-offs related to predation risk (Hebblewhite and Merrill 2007). We have framed predictions of sex-specific time allocation patterns of partially migratory deer to highlight that trade-offs in decision making related to forage maturation and predation risk may differ for males and females (Fig. 1). We found that females were more active than males during the entire growth season and that deer did not seem to behave as strict energy maximizers. To fully understand how this affects individual performance and hence population-level processes, and to predict changes in migratory patterns as well as time allocation patterns within the home range, we need a better understanding of how ecological conditions may affect males and females differently.

Acknowledgments

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