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Back and forth: day–night alternation between cover types reveals complementary use of habitats in a large herbivore

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Abstract

Context The Complementary Habitat Hypothesis posits that animals access resources for different needs by moving between complementary habitats that can be seen as ‘resource composites’. These movements can occur over a range of temporal scales, from diurnal to seasonal, in response to multiple drivers such as access to food, weather constraints, risk avoidance and human disturbance. Within this

framework, we hypothesised that large herbivores cope with human-altered landscapes through the alternate use of complementary habitats at both daily and seasonal scales.

Objectives We tested the Complementary Habitat Hypothesis in European roe deer (*Capreolus capreolus*) by classifying 3900 habitat-annotated movement trajectories of 154 GPS-monitored individuals across contrasting landscapes.

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Methods We considered day–night alternation between open food-rich and closed refuge habitats as a measure of complementary habitat use. We first identified day–night alternation using the Individual Movement - Sequence Analysis Method, then we modelled the proportion of day–night alternation over the year in relation to population and individual characteristics.

Results We found that day–night alternation is a widespread behaviour in roe deer, even across markedly different landscapes. Day–night alternation followed seasonal trends in all populations, partly linked to vegetation phenology. Within populations, seasonal patterns of open/closed habitat alternation differed between male and female adults, but not in juveniles.

Conclusion Our results support the Complementary Habitat Hypothesis by showing that roe deer

adjust their access to the varied resources available in complex landscapes by including different habitats within their home range, and sequentially alternating between them in response to seasonal changes and individual life history.

Keywords Animal trajectories · Habitat use · IM-SAM · Resource composites · Roe deer · Sequential analysis methods · Spatio-temporal patterns · Vegetation green up

Introduction

Fitness is influenced by spatial and temporal heterogeneity in the distribution of multiple, often complementary, resources (Gaillard et al. 2010). A given habitat may not fulfil all the needs of an individual simultaneously, while the functional role of a habitat may fluctuate over time in relation to modifications in an individual's requirements, or in the value of the habitat per se (Peters et al. 2017; Couriot et al. 2018), for example, driven by vegetation phenology. In response, animals may adjust their behaviour through 'complementary habitat use', defined as the use of different habitats at different times by individuals during the course of their daily and seasonal activities (Complementary habitat hypothesis, CHH) (Dunning et al. 1992; Mandelik et al. 2012). For many ungulates, for example, accessibility to forage and protection from predation risk are two key resources that are selected (Hebblewhite and Merrill 2009). Indeed, these two types of resource are both positively related to fitness, but are often spatially distinct (Benhaïem et al. 2008) and fluctuate seasonally, driving complementary use (sensu Mandelik et al. 2012) of 'open' vs. 'cover' habitats (Myrsterud and Østbye 1999; Berlyman and Hawkins 2006). For example, forest canopy can provide cover from adverse conditions (e.g., deep snow: Myrsterud and Østbye 1995, Ewald et al. 2014, Ossi et al. 2015) and protection from predators or human disturbance (Bonnot et al. 2013), while the understorey provides seasonally rich foraging (i.e., during the vegetation green up and re-growth, Mancinelli et al. 2015). In contrast, open areas may be used by ungulates as a seasonal source of forage (Abbas et al. 2011), but mainly at night to avoid human disturbance (Godvik et al. 2009; Bonnot et al. 2013; Dupke et al. 2017; Salvatori et al. 2022), or to

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diminish the risk of ambush predation (Lone et al. 2014; Gehr et al. 2017). Hiding cover may also be seasonally available in open habitats, for example, in summer, when row crops are mature and provide concealing (Mysterud et al. 1997; Bjørneraas et al. 2011; Bonnot et al. 2013; Dupke et al. 2017).

In heterogeneous landscapes, open and closed habitats, hence, may represent composites of different resource types, and animals must alternate between them to satisfy their requirements (see Dunning et al. 1992). Large herbivores use these composites at different spatio-temporal scales, so that the open and closed habitats visited along the movement trajectories generate specific patterns of sequential habitat use (De Groeve et al. 2016). For example, at the daily scale, the day–night alternation between open and closed habitats may be linked to activity cycles e.g., foraging vs. resting and ruminating, or the forage acquisition–predation risk avoidance trade-off (Hebblewhite and Merrill 2009). In turn, daily alternating use of open and closed habitats may vary in relation to seasonal changes in perceived risk (e.g., anthropogenic disturbance, hunting activity; Bonnot et al. 2013, Gehr et al. 2017, 2020), vegetation productivity (i.e., green up and senescence, or cultivation / harvesting; Peters et al. 2019), and physiological cycles (e.g., growth, reproduction, dispersal). The understanding of the complementary use of resource composites across spatio-temporal scales by ungulates could inform managers regarding the functional role of different habitat types in human-modified environments. In particular, the spatial association between open agricultural habitats and forest patches could support thriving populations of wild ungulates in matrix landscapes (Hewison et al. 2009; Linnell et al. 2020). These concepts are well-addressed within the Complementary Habitat Hypothesis framework (Dunning et al. 1992) and well established in ecological theory, but rarely tested for wild populations, especially vertebrates, as most studies concern insects (Mandelik et al. 2012).

Here, we considered the patterns of alternation between open and closed habitats in European roe deer (*Capreolus capreolus*) to test the Complementary Habitat Hypothesis in a highly managed large herbivore (Apollonio et al. 2010) that has successfully adapted to human-modified landscapes (Andersen et al. 1998), including open agricultural areas (Hewison et al. 2009). Roe deer is an ideal

model species to test the Complementary Habitat Hypothesis because it occupies a wide range of landscapes (i.e., different arrangements of complementary habitats, *sensu* Dunning et al. 1992), from completely forested areas to wide open agroecosystems, exhibiting marked behavioural and ecological plasticity (Hewison et al. 1998; Morellet et al. 2013). Moreover, roe deer are known to prefer ecotonal and forest habitats, complemented by the use of open habitats (meadows and crops), typically at night (Bonnot et al. 2013; Dupke et al. 2017), in relation to their bimodal crepuscular activity pattern (Pagon et al. 2013; Krop-Benesch et al. 2013; Bonnot et al. 2020). Finally, roe deer are characterized by sex-dependent space use patterns (Malagnino et al. 2021), especially in spring and summer, when adult males display territorial behaviour (Hewison et al. 1998), and females give birth and care for their young.

We applied the Individual Movement - Sequence Analysis Method (IM-SAM, De Groeve et al. 2020a) to six populations of European roe deer living in contrasting landscapes to evaluate how day–night alternation between closed and open habitats varied across the seasons and environmental contexts. We first hypothesized that day–night alternation between closed and open habitats would mirror the landscape composition (*sensu* Dunning et al. 1992; Table 1: Landscape Composition and Structure Hypothesis, LCSH, H1). In particular, we expected that day–night alternation would occur mainly in heterogeneous landscapes (Table 1: H1, P1). Second, we hypothesized that day–night alternation would also vary seasonally, in relation to the phenology of vegetation (Pettorelli et al. 2006), according to the Complementary Habitat Hypothesis (Mandelik et al. 2012). Specifically, we predicted frequent alternation during vegetation green-up to maximize access to high quality food in rich-open habitats, but less alternation in winter, when meadows and crops provide less food resources and are more exposed to extreme weather conditions (e.g., snow cover, wind exposure; Table 1: CHH, H2, P2.1). Also, we hypothesized that day–night alternation between open and closed habitats would vary over seasons according to key life history events that are linked to sex and age, such as births, or the rut (Table 1: H2, P2.2; Andersen et al. 2000, Bongi et al. 2008). In particular, we predicted that the day–night alternation of females and males should differ the most during the spring–summer season,

Table 1 Summary of hypotheses and analyses (see footnote for abbreviations)

Hypotheses	Predictions	Analysis	Input data
H1: Landscape Composition and Structure Hypothesis (LCSH) <i>“Proportion of alternation between closed and open habitats in roe deer populations depends on the proportion and spatial structure of these habitats in the landscape”</i>	P1 Day-night alternation mainly occurs in heterogeneous landscapes	1. Exploration with mosaic plot 2. GLM—Habitat composition (proportion data; beta distribution); Kruskal Wallis non-parametric comparison M_P: p(closed)~pop 3. GLM – Habitat structure (continuous skewed data; gamma distribution); Kruskal Wallis non-parametric comparison M_ED: edge_density ~ pop 4. GAMMs – Alternation (0/1) (see below) M1: a ~ s(bw * pop) + pop + lbind	Habitat use sequences, classified according to the following patterns: Homogeneous open (o) Homogeneous closed (c) Random (u) Alternation (a)
H2: Complementary Habitats Hypothesis (CHH) <i>“Roe deer alternation between habitats varies seasonally, in relation to environmental and roe deer intrinsic cycles”</i>	P2.1. Within a given landscape, alternation between habitats varies seasonally following the phenology of the vegetation, with more day-night alternation during the vegetation green-up in spring P2.2 Day-night alternation between habitats varies seasonally in relation to intrinsic cycles linked to life-history	1. GAMMs – Alternation (0/1) M1: a ~ s(bw * pop) + pop + lbind 2. ANODEV NDVI $ANODEV = 1 - \frac{L(M_{NDVI}) - L(M_{FULL})}{L(M_{NULL}) - L(M_{FULL})}$ Where: M _{FULL} : a ~ bw * pop + lbind M _{NULL} : a ~ lbind + pop M _{NDVI} : a ~ s(NDVI * pop) + pop + lbind GAMMs – Alternation (0/1) M2: a ~ s(bw * age:sex) + age*sex + lbind	Binomial variable based on the habitat use sequences, defined as follows: c, o, u = 0 a = 1

a = daily habitat alternation (0/1); pop = population; lbind = individual identity as a random effect on intercept; s(bw) = cyclic spline smooth of the biweek; s(NDVI) = cubic spline smooth of the Normalized Difference Vegetation Index; age = fawns & yearlings (< 2 yrs); adults (> 2 yrs); sex = male or female; L = log Likelihood; GAMM; ANODEV

when adult females should alternate less due to the constraints of provisioning for their young (Andersen et al. 2000), while adult males should alternate more to patrol and defend their mating territory, especially during rut (Johansson 1996). Therefore, we expected these sex-specific seasonal patterns to be more evident in adults than juveniles linked to reproductive status and behaviour (Sempéré et al. 1998).

Materials and methods

The habitat use sequences were obtained from roe deer movement trajectories of the Eurodeer database (Urbano and Cagnacci, 2021), as processed in De Groeve et al. (2020a, b), with some simplifications (see below). In the Eurodeer database, roe deer trajectories obtained from GPS collars deployed across European populations are stored and curated together with individual-based information obtained during capture (Urbano and Cagnacci, 2021). In particular, individuals sexed and aged at capture as juveniles (< 1 year old) are considered to become yearlings from 1st April (just before the birth period of roe deer over most of its range) of the year of first monitoring and for the subsequent 12 months. All other individuals are considered adults.

IM-SAM roe deer habitat use sequences and classification as open/closed day–night alternation

To prepare the obtained habitat use sequences, De Groeve et al. (2020a) regularized the roe deer GPS trajectories using a fixed four-hour relocation interval (0, 4, 8, 12, 16 and 20 h) and segmented them into 16-day periods (i.e., referred to as “biweekly” sequences) starting on January 1st (i.e., 01/01–16/01, 17/01–01/02, etc.; 23 biweekly sequences over a year). Then, GPS locations were intersected with the reclassified High-Resolution Raster Layer Tree Cover Density 2012 (TCD, EEA 2012, 20 m spatial resolution), distinguishing closed (C, $TCD \geq 50\%$) and open (O, $TCD < 50\%$) habitats (De Groeve et al. 2020a). These sequences were then classified following the IM-SAM procedure, where sequences of observed habitat use were clustered together (i.e., classified or ‘tagged’) with sequences of simulated habitat use, reflecting specific patterns of sequential habitat use. The final data contained the following

patterns of sequential habitat use: homogeneous closed (c), homogeneous open (o), day–night alternation between closed and open habitats (a) and random (u). Seasonal and latitudinal changes in day length were accounted for when classifying day–night alternation (De Groeve et al. 2020a). The final classification of sequences into these four patterns of sequential habitat use is illustrated for two representative populations in Fig. 1 (see also Appendix S1, Figure S1.2 for the final classification of all populations). From the resulting dataset, we extracted the data for six roe deer populations with a representative number of individuals (≥ 10 individuals): Southern France (Eurodeer database study area identifier: FR8), Switzerland (CH25), Southern Germany (DE15), Southeast Germany (DE2), and Northern Italy (IT1, IT24; see Figure S1.1, Table S1.2 for a description of each population). Because we were interested in modelling seasonal variations in day–night alternation, we removed individuals which had less than 10 biweekly habitat use sequences. Our final dataset consisted of 3900 habitat use sequences from 154 animals (95 females and 59 males, made up of 44 juveniles/yearlings and 132 adults, with 22 animals switching from fawns to adults during monitoring; Table S1.2).

Covariates linked to roe deer habitat use sequences

To test whether day–night alternation is linked to vegetation phenology, we computed the landscape level vegetation productivity profile for each biweekly period estimated by the Normalized Difference Vegetation Index (NDVI; smoothed and pre-processed as in Vuolo et al. 2012) using the following workflow. First, we defined the study area as the Minimum Convex Polygon (MCP) of all locations from all individuals within a population. For each population’s MCP, we sampled 1000 random points within that area (corresponding to a survey density of 1.06 ± 0.06 points per hectare, average \pm standard deviation) and extracted the weekly NDVI values. Next, we matched each biweekly period with the corresponding averaged weekly NDVI values.

Sequential habitat use through space: landscape composition and structure hypothesis (H1)

First, we investigated the variation in the proportion of habitat use sequences across populations.

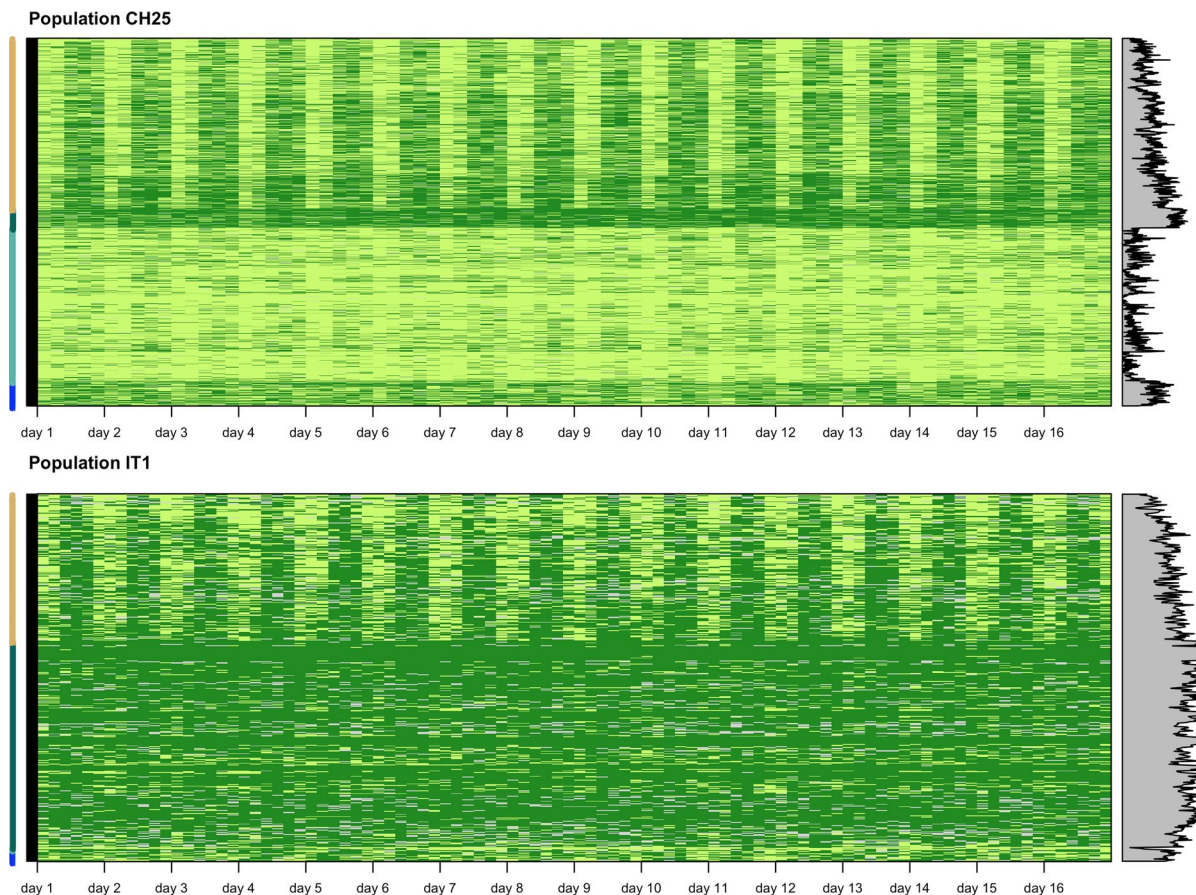


Fig. 1 The IM-SAM classification of biweekly habitat use sequences (light green, open habitat; dark green, closed habitat) in the four sequential patterns: daily alternation (color of the y-axis: light brown), homogeneous closed (dark green), homogeneous open (turquoise) and random (blue), for ani-

mals ranging in mainly open (CH25, Switzerland) and mainly closed (IT1, Northern Italy) landscapes. Aligned on the right: *proportion* of closed habitat used for each sequence. See Figure S1.2 for all populations

The input for this analysis consisted of an abundance table of patterns of sequential habitat use (day–night alternation, a; homogeneous closed, c; homogeneous open, o; random, u) per population. The results were visualized using a mosaic plot, along with a chart indicating the proportion of closed habitat and closed and open edge density (as a proxy of landscape fragmentation) for each population, a circular map extract covering the population range and the number of individuals and sequences (Fig. 2). To test the Landscape Composition and Structure Hypothesis (H1), we first verified whether the probability of alternation varied across landscapes. We expressed habitat alternation as a binomial variable where day–night alternation (a)

is 1 and all other patterns of sequential habitat use (c, o, u) are 0. We built Generalized Additive Mixed Models (GAMMs) with a binomial distribution of residuals, with day–night alternation as the response variable, the cyclic spline smooth of the biweek to account for temporal variation, and population as a fixed (ordered) factor, or as a factor-specific temporal effect (e.g., a population-specific spline of biweek; M1, see below and Table 1: H1; H2.1). We included individual identity as a random effect on the intercept. The most parsimonious model was selected based on minimization of the Akaike Information Criterion (Burnham and Anderson 2002). Second, we compared the landscape composition between populations, measured as proportion of

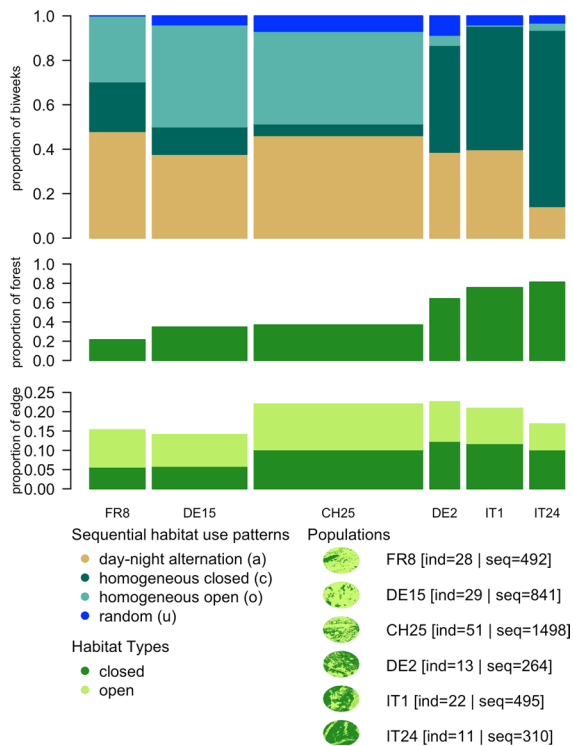


Fig. 2 Mosaic plot of the proportion of different daily sequential habitat use patterns (first panel), bar plots of the proportion of closed habitat (second panel) and the proportion of open and closed edge per hectare (third panel) in each population (codes along the x-axis of the third panel). The number of individuals (ind) and the number of sequences (seq) for each population are shown in the bottom panel. Further, a visualization of the open-closed landscape composition is presented as circles (study area codes as in main text; see also Appendix S1)

closed habitat, closed edge and open edge densities. To do that, for each population's MCP, we sampled 1000 random points within that area, buffered them with a 200 m radius, and measured these metrics. We built a Generalized Linear Model (GLM) with proportion of closed as the response variable with beta distribution of residuals, and population as a fixed (ordered) factor; and two GLMs with open edge and closed edge density, respectively, as response variables with gamma distribution of residuals, and population as a fixed (ordered) factor. We also applied the non-parametric Kruskal–Wallis

test to each variable separately, using the measures in the buffers as repetitions, grouped by population, as a further confirmation of the robustness of the analysis. The Landscape Composition and Structure Hypothesis (H1) cannot be supported if a clear link between the probability of alternation and landscape composition and structure cannot be established, for example if the probability of alternation does not vary across populations, but the composition and structure of landscape is different. The GLM analyses were performed in R 4.0.0 (2020-04-24) with the package `glmmTMB` (Brooks et al. 2017).

Sequential habitat use through time: Complementary Habitats Hypothesis (H2)

For this set of analyses, we used habitat alternation as a binomial variable, defined as above. We built two Generalized Additive Mixed Models (GAMMs) with a binomial distribution of residuals, with day–night alternation as the response variable, the cyclic spline smooth of the biweek to account for temporal variation, and a given predictor (Model 1, M1: population—see also H1; Model 2, M2: age x sex) for each set of models, as a fixed (ordered) factor, or as a factor-specific temporal effect (e.g., population or sex/age class-specific spline of biweek). In all models, we included individual identity as a random effect on the intercept (see full models in Table 1: H2.1 and H2.2). The most parsimonious model was selected based on minimization of the Akaike Information Criterion (Burnham and Anderson 2002). For the population model (M1), we subsequently used the ANODEV procedure (Grosbois et al. 2008) to quantify the proportion of variation in day–night alternation that was accounted for by NDVI (see Table 1, H2.1 for the formula). For visual purposes, we also modelled the annual pattern of NDVI (see Fig. 3) using a GAMM with the exact same model structure as M1 (i.e., population-specific cyclic spline smooth of the biweek, with individual identity as a random effect on the intercept), but with the population-level NDVI value of the sequence as the response variable. All statistical analyses were performed in R 4.0.0 with the packages `mgcv` (Wood 2017) and `visreg` (Breheny and Burchett 2017).

Results

Sequential habitat use through space: landscape composition and structure hypothesis (H1)

Visually, the proportion of the four sequential habitat use patterns was not characterised by the populations. Indeed, although the homogeneous closed (c) and homogeneous open (o) sequential habitat use patterns were specific to certain populations (Fig. 2), the day–night alternation (a) was present in all populations, with approximately 40% of all habitat use sequences (38–47%) classified as such, except when

closed habitats were widely prevalent (in population IT24, 14%; Fig. 2). This was statistically confirmed by the fact that the probability of alternation did not depend on population (i.e., as a fixed effect; Table 2a, Table S3.2), but only its temporal variation did (i.e., interaction between spline of biweek and population). Random sequential habitat use patterns (u) were rarely observed in any population.

In contrast, landscape composition (i.e., proportion of closed habitats) differed across populations (GLMM - ref. level: FR8, IT1: 2.13, SE 0.05, $p < 0.001$, DE2: 1.31, SE 0.06, $p < 0.001$, DE15: 0.15 SE 0.05, $p < 0.001$, IT24 2.26, SE 0.06, $p < 0.001$,

Table 2 Approximate significance of smoothing terms and fixed effects in the selected model (a. cyclic spline of biweek per population, AIC = 3777.7, adj $R^2 = 37.1$; b. cyclic spline of

biweek per modality of the age and sex interaction term, added as a fixed factor, and the spline of the biweek, AIC = 3837.9, adj $R^2 = 35.2$)

(a)	edf	Ref df	Chi.sq	p	
s(biweek): population CH25	6.965	8	1878.5	<0.0001	***
s(biweek): population DE15	6.288	8	2935.4	<0.0001	***
s(biweek): population DE2	6.582	8	2182.9	<0.0001	***
s(biweek): population FR8	6.015	8	1660.0	<0.0001	***
s(biweek): population IT1	4.733	8	238.0	0.0499	*
s(biweek): population IT24	6.242	8	768.3	<0.0001	***
individual	144.473	148	663.7	<0.0001	***
	Estimate	sd	z	P	
intercept	-1.174	1.715	-0.102	0.919	
DE15	-1.270	2.860	-0.444	0.657	
DE2	-2.012	3.833	-0.525	0.600	
FR8	-0.321	2.906	-0.111	0.912	
IT1	-1.182	3.137	-0.377	0.706	
IT24	-2.860	4.093	-0.699	0.485	
(b)	edf	Ref df	Chi.sq	p	
s(biweek)	6.753	8	2006.048	<0.001	***
s(biweek): ordered(sex*age) juvenile female	1.115	8	23.331	0.169	
s(biweek): ordered(sex*age) adult male	3.228	8	2639.053	<0.001	***
s(biweek): ordered(sex*age) juvenile male	0.002	8	0.001	0.513	
individual	148.501	152	732.484	<0.001	***
	Estimate	sd	z	P	
intercept	-1.0681	1.2351	-0.865	0.387	
juvenile female	0.2464	0.3259	0.756	0.450	
male	0.3487	1.9989	0.174	0.862	
juvenile male	-0.0238	2.0079	-0.012	0.991	

To better assess age and sex differences, we provide the general time-dependent model, followed by the age and sex differences from this general model. The latter model gives the same results as the M1 model in Table 1, which was used in the predictions of Fig. 4. Both models include individual identity as a random effect on the intercept to avoid pseudo-replication

CH25: 0.34 SE 0.05, $p < 0.001$; res dev = -10665.4; β disp par = 1.11; Kruskal–Wallis test for proportion of closed habitats: chi-squared = 2213.5, $df = 5$, $p < 0.0001$; also confirmed by pairwise post-hoc t tests between all pairs of populations), such that some populations were mainly ranked as ‘closed’ (IT24, IT1 and DE2; median proportion of closed: 0.94, 0.85, 0.74, respectively), while others as ‘open’ (CH25, DE15 and FR8; median proportion of closed: 0.30; 0.18; 0.13). Similarly, landscape structure (i.e., closed and open edge densities) was overall different across populations, however non-significant differences between paired populations were observed (open edge density, GLMM - ref. level: FR8, IT1: -573.8, SE 549.8, n.s., DE2: -2203.5 SE 501.1, $p < 0.001$, DE15: 2641.0 SE 660.3, $p < 0.001$, IT24 5881.1 SE 785.0, $p < 0.001$, CH25: -3092.3 SE 477.6, $p < 0.001$; res dev = -100044.3; $\sigma^2 = 2.15$; Kruskal–Wallis test = 1597.0, $df = 5$, $p < 0.0001$; pairwise post-hoc t-test n.s. for: IT24/CH25 and DE15/FR8; closed edge density, GLMM - ref. level: FR8, IT1: -13645.4 SE 830.4, $p < 0.001$, DE2: -14136.5 SE 825.0, $p < 0.001$, DE15: -568.9 SE 1113.4, n.s., IT24 -11444.3 SE 860.1, $p < 0.001$, CH25: -11717.0 SE 855.9, $p < 0.001$; res dev = -98804.0; $\sigma^2 = 1.77$;

Kruskal–Wallis = 1021.7; $df = 5$; $p < 0.0001$; pairwise post-hoc t-test n.s. for: DE15/IT1).

Hence, our results do not support the hypothesis that day–night alternation simply mirrors landscape composition and structure, or that alternation is limited to highly heterogeneous landscapes (Table 1: P1).

Sequential habitat use through time: Complementary Habitats Hypothesis (H2)

The probability of day–night alternation varied over the year with contrasting seasonal patterns among populations, as shown by the interaction between the cyclic spline smooth of the biweek being in interaction with population retained in all the best models to explain the temporal pattern of alternation (Fig. 3 and Table 2a, AIC = 3777.70, $\Delta AIC = 146.0$ with the second best model, R^2 (adj.) = 0.37; Table S2.1 for model selection results).

In all six populations, the probability of day–night alternation followed a bimodal pattern, with an increase in early spring (between late March and late May, from 6th to 9th biweek), followed by a drop in late spring (between mid-May and mid-July, from 9th to 12th biweek), and a second increase in

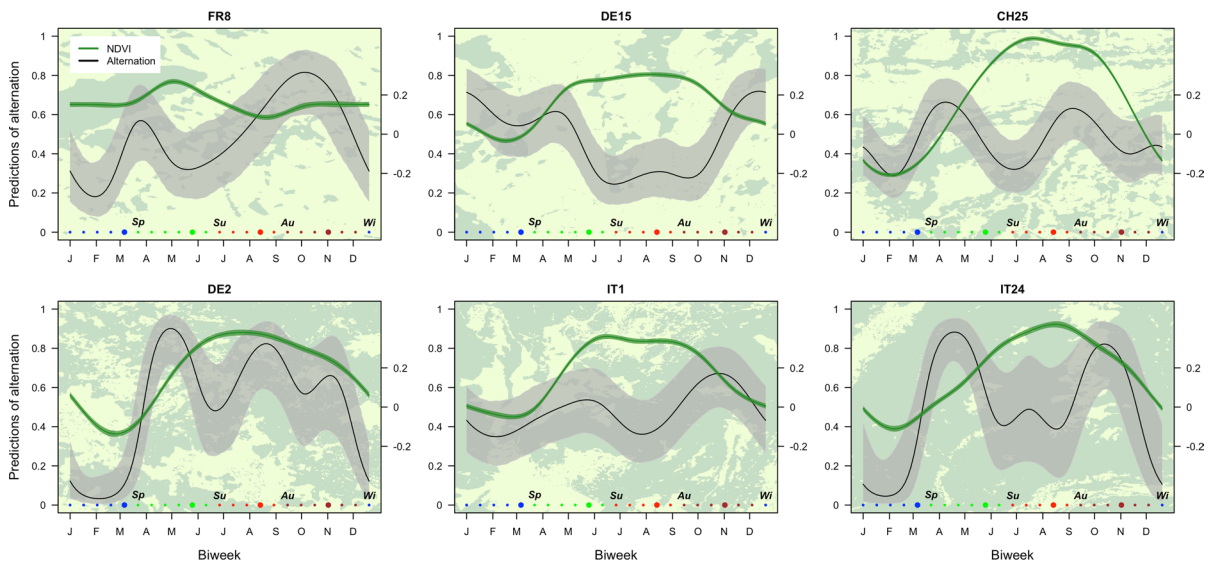


Fig. 3 Predictions for the probability of habitat alternation between open and closed habitats by roe deer in the six populations over biweekly periods of the year. The smoothed averaged annual NDVI pattern is overlaid as a second y-axis. The sampling units for both curves are biweeks (dots colored

by season; blue: winter; green: spring; red: summer; brown: autumn; a larger dot indicates every other fifth biweek; months indicated on x-axis for readability). The background of the panels represents the landscape (open habitat in light green vs. closed habitat in dark green) of the respective study area

early autumn (between mid-August and mid-November, from 18th to 20th biweek). However, while a decrease in day–night alternation between mid-January and early-March (2nd and 4th biweek) occurred in all populations, alternation was more frequent in winter (Dec. – May), before falling in summer (May – Dec.) in South-Germany (DE15: Fig. 3, top-central plot). We found that 44% of the variation in day–night alternation across the year was explained by NDVI (Table S3.1; ANODEV). In particular, the first spring peak in day–night alternation generally corresponded to the steepest positive slope of the modelled NDVI curves (in turn varying across populations: best model including the spline of the interaction between biweek and population, Table S3.2; $\Delta\text{AIC}=7754.4$ with the second-best model) i.e., the spring vegetation green up in each study site (Fig. 3, overlaying NDVI curves). Our results, thus, support the prediction that day–night alternation is not a fixed property at the landscape level, but varies in time to track seasonal cycles of vegetation phenology, such as green up or harvesting (Table 1: H2.1, P2.1).

We also found that the seasonal pattern in the probability of day–night alternation was significantly different between adult females and males (Fig. 4, left panel and Table 2b; $\text{AIC}=3837.9$, $\Delta\text{AIC}>12.0$ with all other models, $R^2(\text{adj.})=0.35$; Table S2.1). While the temporal pattern followed a similar general

pattern, adult females alternated less than adult males during the summer (Fig. 4, left panel: probability of alternation for females=0.29 (CI: 0.20–0.42) vs. males=0.59 (CI: 0.40–0.76) at the end of June–12th biweek). On the contrary, adult females alternated more than adult males during winter i.e., from late December to early March (probability of alternation for females=0.49 (CI: 0.34–0.63) vs. males=0.18 (CI: 0.09–0.34) during the 3rd biweek). During other parts of the year, the confidence intervals of the predictions overlapped strongly, indicating little difference in habitat alternation between sexes. Our model also showed that the seasonal pattern in the probability of day–night alternation was not significantly different between female and male juveniles (Fig. 4, right panel; Table 2b; Table S2.1). Specifically, the temporal pattern of alternation in juveniles of both sexes followed the same trend as that of adult females. Overall, we thus found some support for the hypothesis that temporal variation in alternation between habitats is also linked to life-history constraints (Table 1: H2.2, P2.2). Finally, the two-way interaction between age and sex did not feature in the retained model as a fixed factor, indicating that the average overall amplitude in alternation across the year did not vary between factor-levels.

In all models, the ‘individual’ random effect (i.e., including individual identity as a random effect on the

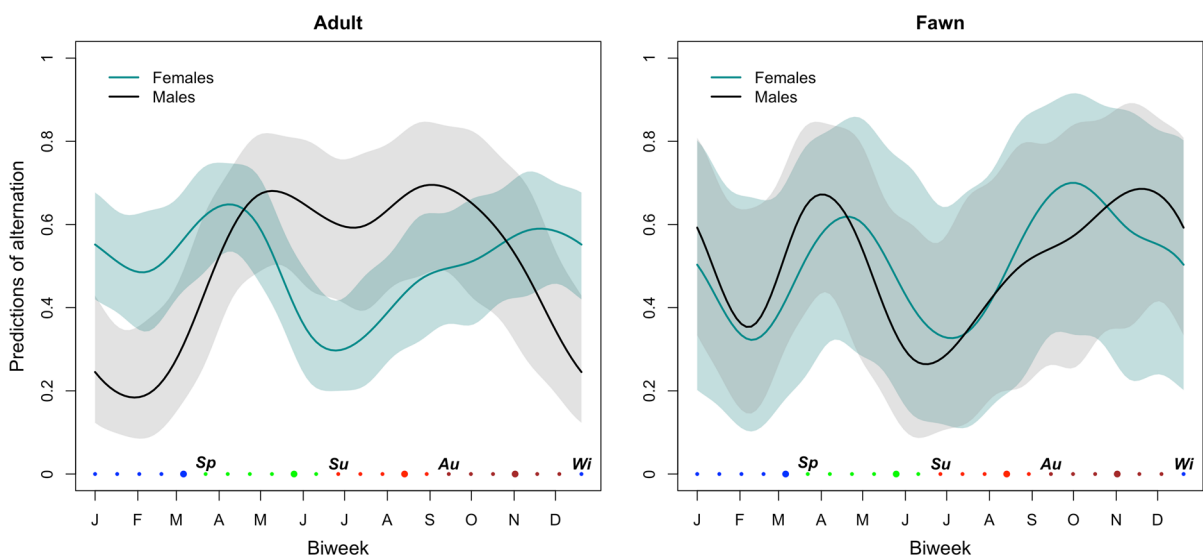


Fig. 4 Predictions for the probability of day–night habitat alternation between open and closed habitats by roe deer according to sex and age (left panel: female/male adults; right panel: female/male fawns) over biweekly periods of the year. x-axis as in Fig. 3

intercept) contributed considerably towards explaining the variance (R^2 (adj.) $_{\text{NULL model}} = 0.31$; see Table S2.1), indicating marked inter-individual variability in habitat alternation within a given population.

Discussion

In spatially heterogeneous environments, wild animals must access various resources with different spatial distributions and, often, asynchronous phenology. Our analysis shows that day–night alternation between open and closed habitats is a prevalent characteristic of roe deer movement tactics across a wide range of landscapes with contrasting composition and spatial arrangement (Dunning et al. 1992; H1 overall not supported). The most likely explanation of this behaviour is that animals use day–night alternation to access food and cover in these resource composites (Padié et al. 2015; Bonnot et al. 2018). The observed seasonal variation in day–night alternation within a given landscape supports this interpretation. Roe deer likely exploit the diversity of resources offered by those habitats at different times of the year, and according to their needs (Mandelik et al. 2012). Our results indirectly support the Complementary Habitats Hypothesis (H2) by showing marked cycles of day–night alternation over the seasons (H2.1), with clear differences between the adult sexes (H2.2).

Understanding the complexity of animal resource requirements and consequent habitat use is important as it affects a range of ecosystem processes. The frequent alternation between habitats documented here likely affects transportation of seeds and nutrients between cultivated and more natural habitats (Abbas et al. 2012; Earl and Zollner 2017 for an example on roe deer), as well as spatial dynamics of parasites, including vectors of vector-borne zoonotic pathogens (Carpi et al. 2008; Mysterud et al. 2017; Chastagner et al. 2017). Further, such habitat alternation may influence human-wildlife interactions relevant for management, from harvesting efficiency and forest damage, to road-crossing and risk of deer-vehicle collisions (Hothorn et al. 2015; Passoni et al. 2021). Indeed, in highly anthropogenic European landscapes, the availability of essential resources for free-ranging large herbivores – food and cover – vary both naturally (i.e., due to phenological cycles of vegetation, Pettorelli et al. 2006), and as a consequence of human

activities (e.g., agriculture and forest management practices; Lande et al. 2014). In this context, large herbivores must continually adjust their use of habitat to these changes, trading off access to resources and protection from predators and human disturbance (Godvik et al. 2009; Gehr et al. 2017). Several studies have shown that ungulates in temperate environments modulate habitat selection at different spatial (e.g., Boyce et al. 2003, DeCesare et al. 2014) and temporal scales, especially diel and seasonal scales (Dupke et al. 2017; Roberts et al. 2017; Martin et al. 2018). Yet, comparisons across contrasted environmental contexts are rare, limiting the possibility for testing hypotheses on the behavioural responses to landscape-level heterogeneity. In this work, we were able to test two alternative hypotheses on diel habitat alternation by comparing the occurrence of this behaviour spatially (across landscapes) and temporally (across seasons). According to our results, the order in which habitats were used varied over the year and across life history stages, likely in relation to different resource needs and constraints (De Groot et al. 2020a).

Temporal variation in alternation between open and closed habitats is likely due to a complementary functional use of habitats that occur within the home range (Dunning et al. 1992; Mandelik et al. 2012; Couriot et al. 2018). In our study, individuals in most populations alternated between open and closed habitats more frequently in spring, possibly due to earlier green-up in open habitats, with fresh high-quality herbaceous vegetation (Abbas et al. 2011; Dupke et al. 2017), and in the fall, perhaps due to the availability of plants with delayed leaf loss or crop stubble in open habitats. Indeed, we found that about half of the temporal variation in the probability of alternation between open and closed habitats was explained by variation in the population-level NDVI value (Fig. 3). A recent large-scale study on several boreal ungulate species showed that roe deer tended not to move across the landscape to ‘surf’ the green wave, instead, they maximized the ‘greenness’ quality of their ranges (Aikens et al. 2020). Alternating between habitats could be a tactic to achieve such maximization locally, accessing complementary resources in different habitat types (see also Peters et al. 2017).

In winter, individuals in study areas with substantial forest cover (mainly IT24, DE2; Fig. 3) alternated less, and showed, instead, a consistent and more homogeneous use of closed habitats at a time when

forest habitat provides thermal protection, shallower snow (Myserud et al. 1997; Myserud and Østbye 2006; Ratikainen et al. 2007; Ossi et al. 2015), and potentially higher food availability, either more abundant vegetation forage or supplementary food provided by hunters (Ewald et al. 2014; Ossi et al. 2017), compared to open habitats. Interestingly, the population in the agricultural landscape of Southern Germany (DE15; Fig. 3) exhibited the opposite pattern to all others, with more pronounced alternation in winter, followed by a consistent and homogeneous use of open habitats in summer. This behaviour could be due to cover-food complementation: roe deer may access open areas at night in winter to consume winter grain (no cover but valuable food resource), while using open habitat both as a food and cover source in summer, when crops are abundant in the fields and can also provide hiding cover (Bonnot et al. 2013). This pattern was not observed in Southern France (FR8), a landscape also consisting of patches of forest within an agricultural matrix. This could be due to different agricultural practices and levels of disturbance, but also because of the use by deer of small cover features in open landscapes such as tree patches and hedgerows that are not defined as forest by the forest cover layer (TCD; <https://land.copernicus.eu/user-corner/technical-library/hrl-forest>). In this paper, we used a high resolution (20 m), but static and simplified, classification of open and cover habitats. However, habitat alternation may also occur between different habitat classes (such as pastures, agricultural fields), or between forest units with different forest cover thresholds (in very dense landscapes). This suggests that roe deer compensate their need for cover within a given landscape with different types of ‘functional cover’ (Myserud and Østbye 1999).

To better evaluate these hypotheses, future studies should look into fine-scale variation in alternation behaviour (see Couriot et al. 2018), while explicitly accounting for the spatio-temporal availability of anthropogenic resources (Ossi et al. 2017; Ranc et al. 2020) and their revisitation patterns (Ranc et al. 2021, 2022). As temporally dynamic remote sensing products indexing the composition and structure of habitats become increasingly available (Pettorelli et al. 2014; Neumann et al. 2015; Oeser et al. 2020), alternation between habitats could be more mechanistically linked to the resources they offer, revealing their functional role at different spatio-temporal scales

(Godvik et al. 2009; Mandelik et al. 2012; Couriot et al. 2018). For instance, identification of cover vs. non-cover could be improved by quantifying habitat visibility explicitly through LiDAR surveys (Zong et al. 2022).

Among-individual variation within population also seems to be a strong driver of alternation patterns that could be linked to intrinsic individual characteristics like age and sex, but also personality traits (or behavioural types) (Bonnot et al. 2015). We found a link between the temporal pattern of alternation and the sex of individual adult roe deer, with a clear contrast in the degree of day–night alternation between open and closed habitats during summer (more alternation in males) and during the winter (more alternation in females). Mammals have a timing and intensity of resource allocation to reproduction that differs by species, and sex (Williams et al. 2017). For example, the separation of sexes outside of the mating season, termed sexual segregation, is a wide-spread phenomenon among ungulates. Segregation in diet and habitat increase with higher sexual body size dimorphism, due to that body size markedly affect digestion and dietary requirements of ruminants (Myserud 2000). Here we suggest an alternate form of adaptation to sex-specific needs, namely the diel order in the use of cover and open-habitat resources, that may not emerge as spatial separation. Despite roe deer being one of the few ungulates with a low degree of sexual size dimorphism, there are marked sex-specific differences in behaviour in spring–summer. Males are territorial from March until the rut in July–August (Sempéré et al. 1998), while females give birth in May or early June, allocating heavily to late gestation and early lactation during summer. Alternation between open and closed habitats was twice as high in males than females during the birth season and the period of intensive maternal care. Movement rate has also been shown to decrease during this period (Malagnino et al. 2021), possibly because of spatial constraints imposed by suckling newborn fawns. In contrast, males maintained a higher degree of habitat alternation throughout the summer, likely linked to territory patrolling and defence (Linnell and Andersen 1998; Malagnino et al. 2021). The fact that these sex-specific patterns were observed in adults, but not fawns, highlights how different habitat use of the sexes can arise from sex-specific schedules of allocation to reproduction. Sex-specific habitat alternation

is inversed during winter, such that females alternate around three times more than males between December and March. This marked effect, and particularly the switch compared to the summer pattern might be related to a difference in the perception of risk between males and females linked to hunting practices (Benhaïem et al. 2008). The selective hunting pressure on male roe deer is suddenly reduced after they drop their antlers in November, to become higher for females, instead. This hypothesis should be tested in future research.

The survival and reproductive performance of large herbivores depends strongly on the use of, or, as we suggest here, alternation, between habitats that are rich enough to ensure the necessary energy intake but are also safe enough to provide protection against predators (Gaillard et al. 2000). Daily habitat use in large herbivores, in particular, has been linked to circadian activity cycles (Pagon et al. 2013), to the food-cover trade-off (van Beest et al. 2013), including thermal cover (Myrsterud and Østbye 1999), and to rumination cycles, where the use of cover is higher during rumination than during feeding bouts (Cederlund 1981). In this study, we showed how investigating daily alternation between habitat types may provide insights into the complementation in resource needs at different spatio-temporal scales and in relation to life-history constraints.

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Author contributions JDG conducted the research and conceived the study idea and the study design together with FC and NVdW. NM, NCB, AJMH, BG, MH, MK, and FC provided the datasets. The progress of the study was discussed in the context of Eurodeer meetings and working groups with all co-authors. JDG, FC, NR, NM conducted the data analyses. The first draft of the manuscript was written by JDG and FC and critically commented and reviewed by all co-authors. All authors read and approved the final manuscript.

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Data availability Unfiltered classified sequences are available on Zenodo at <https://doi.org/10.5281/zenodo.1254230>. Additional associated variables (sex, age, NDVI) were retrieved from the EUROMAMMALS spatial database hosted by the Fondazione Edmund Mach (<https://euromammals.org>) and can be accessed upon login. The subset of the data and scripts used in the current analyses will be made available on Zenodo upon acceptance.

Declarations

Ethics Approval Roe deer captures and collaring were compliant to national and international welfare regulations, and approved as follows. SE-Germany (DE2): The research program in the Bavarian Forest is managed by the Administration of the Bavarian Forest National Park. Game captures were conducted in accordance with European and German animal welfare laws. The experiment was designed to minimize animal stress and handling time, and to ensure animal welfare, as defined in the guidelines for the ethical use of animals in research. Animal captures and experimental procedures were approved by the Ethics Committee of the Government of Upper Bavaria and fulfils their ethical requirements for research on wild animals (Reference number 55.2-1-54-2531-82-10); N-Italy (IT1, IT24): animal handling practice, such as captures and collar marking, complied with the Italian laws on animal welfare and has been approved by the Wildlife Committee of the Autonomous Province of Trento, 09/2004S; Switzerland (CH25): The animal capture and handling protocols were authorized by the cantonal veterinary and animal welfare services with permit number BE75/11; SW-France (FR8): prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection; SW-Germany (DE15): The animal capture and handling protocols were authorized by the animal welfare and hunting administra-

tion of the federal state of Baden-Wuerttemberg, Germany (RP Freiburg; G-09/53).

Conflict of interest The authors declare no competing interests.

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