

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 on a range of temporal scales, from diurnal to seasonal, responding to multiple drivers, such as access to food, weather constraints, risk avoidance, human disturbance. Within this framework, we hypothesised that large herbivores may 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.

Methods

We considered day-night alternation between food-rich open and closed refuge habitats as a proxy for complementary habitat use. We first identified day-night alternation by using IM-SAM, 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 the alternate use of habitats in response to changes in resource availability and individual needs. By repeatedly crossing habitat boundaries large herbivores may "engineer" their landscape by transporting seeds, parasites and nutrients between those habitats.

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 animal 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. Mandelik et al. (2012) defined 'complementary habitat use' as the use of different habitats at different times by individuals during the course of their daily and seasonal activity (Complementary Habitat Hypothesis, CHH). For many ungulates, for example, accessibility of forage acquisition and protection from predation risk are two key resources that are selected (Hebblewhite and Merril 2009). Indeed, these two types of resource are both positively related to fitness, but often spatially distinct (Benhaiem et al. 2008) and temporally variant, driving complementary use (sensu Mandelik et al. 2012) of 'open' vs 'cover' habitats (Mysterud and Ostbye 1999, Berryman and Hawkins 2006). For example, forest canopy can provide cover from adverse conditions (e.g., deep snow: Mysterud and Ostbye 1995, Ewald et al. 2014, Ossi et al. 2015) and protection from predators or human disturbance (Gehr et al. 2020), 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, but mainly at night to avoid human disturbance (Godvik et al. 2009, Bonnot et al. 2013, Dupke et al. 2017, Bonnot et al. 2020), or to diminish the risk of ambush predation (Lone et al. 2014; Gehr et al. 2020). Hiding cover may also be seasonally available in open habitats, for example, in summer, when crops are high (Mysterud et al. 1997, Bjørneraaas et al. 2011, Bonnot et al. 2013, Dupke et al. 2017).

In temperate ecosystems, open and closed habitats, hence, may represent composites of different resource types, and animals have to 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 used along the movement trajectories generate specific patterns of sequential habitat use (De Goeve et al. 2016). For example, at the daily scale, the day-night alternation between open and closed may be linked to activity cycles e.g., foraging vs. resting and ruminating, or forage acquisition-predation risk avoidance trade-off (Hebblewhite and Merril 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; Gehr et al. 2017, Bonnot et al. 2020), vegetation productivity (i.e., green up and senescence, or cultivation / harvesting; Peters et al. 2019), and physiological cycles (e.g., growth, reproduction, dispersal; Bonnot et al. 2018). 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. For example, 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 and well established in ecological theory, but rarely tested for wild populations.

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 (Hewison et al. 2009), including open agricultural areas (Andersen et al. 1998). 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* Dunnings et al. 1992), from completely forested areas to wide open agroecosystems, exhibiting marked behavioural and ecological plasticity (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-based Sequence Analysis Method (IM-SAM, De Goeve 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* Dunnings 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, such as reproduction, and other physiological constraints that are linked to sex and age (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 reproductive season, when adult females should alternate less due to the constraints of maternal care (Andersen et al. 2000), while adult males should alternate more to patrol and defend their mating territory (Johannson et al. 1996). Therefore, we expected these seasonal patterns to be more evident in adult males than juveniles linked to reproductive status (Sempéré et al. 1998).

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

Hypotheses	Predictions	Analysis	Input data
H1: Landscape Composition and Structure Hypothesis (LCSH) "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"	P1 Day-night alternation mainly occurs in heterogeneous landscapes	Exploration with mosaic plot and non-parametric statistics based on overall frequencies of habitat use sequences in each population, related to the open/closed composition and structure.	Habitat use sequences, classified according to the following patterns: Homogeneous open (o) Homogeneous closed (c) Random (u) Alternation (a)
H2: Complementary Habitats Hypothesis (CHH) "Roe deer alternation between habitats varies seasonally, in relation to environmental and roe deer intrinsic cycles"	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: $a \sim s(bw * pop) + pop + 1 ind$ 2. ANODEV NDVI $ANODEV = 1 - \frac{L(M_{NDVI}) - L(M_{NULL})}{L(M_{FULL})}$ $a = 1$ Where: $M_{FULL}: a \sim bw * pop + 1 ind$ $M_{NULL}: a \sim 1 ind + pop$ $M_{NDVI}: a \sim s(NDVI * pop) + pop + 1 ind$ GAMMs – Alternation (0/1) M2: $a \sim s(bw * age:sex) + age*sex + 1 ind$	Binomial variable based on the habitat use sequences, defined as follows: $C_o = 0, H = 0$

1 **a** = daily habitat alternation (0/1); **pop** = population; **1|ind** = 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

Material 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 Goeve 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 fawns (< 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 Goeve 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, 20m spatial resolution), distinguishing closed ($C, TCD \geq 50\%$) and open ($O, TCD < 50\%$) habitats (De Goeve 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 Goeve 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 fawns/yearlings and 132 adults; 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 extracted the weekly NDVI values of 1000 random points sampled within that area. 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. The input for this analysis consisted of an abundance table of patterns of sequential habitat use (a, c, o, u) per population. The results were visualized using a mosaic plot, along with a chart indicating the proportion of closed habitat and 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). Second, we performed a non-parametric Friedman test (Hollander and Wolfe 1973) to compare the proportion of patterns of sequential habitat use across populations.

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

For this set of analyses, 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 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; 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., a population-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 3.4.4 (2018-03-15) with the packages mgcv (Wood 2017) and visreg (Breheny and Burchett 2017).

Results

Sequential habitat use through space: Landscape Composition and Structure Hypothesis, H1

The proportion of the four sequential habitat use patterns was only marginally different across populations (Friedman-test, Friedman chi-squared = 6.3; df = 3; p = 0.10). Indeed, the homogeneous closed (c) and homogeneous open (o) sequential habitat use patterns were specific to certain populations (Fig. 2), but day-night alternation (a) was present in all populations, with approximately 40% of all habitat use sequences classified as such, except when closed habitats were widely prevalent (in population IT24; Fig. 2). In contrast, random sequential habitat use patterns (u) were rarely observed across all populations. Hence, our results do not fully support the hypothesis that day-night alternation simply mirrors the landscape composition and structure (Table 1: P1).

Sequential habitat use through time: Complementary Habitats Hypothesis, H2

The probability of day-night alternation varied over the year (cyclic spline smooth of the biweek included in all the best models to explain the temporal pattern of alternation; see Table S2.1 for model selection results), with contrasting seasonal patterns among populations (Fig. 3 and Table 2a, AIC = 3777.70, ΔAIC = 146.0 with the second best model, R^2 (adj.) = 0.37; Table S2.1).

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 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; ΔAIC = 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 female and male adults (Fig. 4a and Table 2b; AIC = 3837.9, ΔAIC > 12.0 with all other models, R^2 (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. 4a: probability of alternation for females = 0.29 [C.I.: 0.20–0.42] vs males = 0.59 [C.I.: 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 [C.I.: 0.34–0.63] vs males = 0.18 [C.I.: 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 fawns (Fig. 4b, Table 2b; Table S2.1). Specifically, the temporal pattern of alternation in fawns of both sexes followed the same trend as that of female adults. 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).

In all models, the random effect of ‘individual’ (i.e., including individual identity as a random effect on the intercept) contributed considerably towards explaining the variance (R^2 (adj.)_{NULL model} = 0.31; see Table S2.1), indicating marked inter-individual variability in habitat alternation within a given population. Finally, the fixed effects for population or the interaction between age and sex were not significant, indicating that on average alternation did not vary between respective factor-levels.

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 R² = 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 R² = 35.2). 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.

(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	***
animal	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) female fawn	1.115	8	23.331	0.169	
s(biweek) : ordered(sex*age) male adult	3.228	8	2639.053	< 0.001	***
s(biweek) : ordered(sex*age) male fawn	0.002	8	0.001	0.513	
animal	148.501	152	732.484	< 0.001	***
	estimate	sd	z	P	
intercept	-1.0681	1.2351	-0.865	0.387	
female fawn	0.2464	0.3259	0.756	0.450	
male	0.3487	1.9989	0.174	0.862	
Male fawn	-0.0238	2.0079	-0.012	0.991	

Discussion

In spatially heterogeneous environments, wild animals must access multiple resources with different spatial distributions and, often, asynchronous phenology. Our analysis has shown that the 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 (Dunnings et al. 1992; H1 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). 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 clear cycles of day-night alternation over the seasons (H2.1), with clear differences between the adult sexes (H2.2).

In the highly anthropogenic European landscape, the availability of essential resources for free-ranging large herbivores – food and cover – vary naturally (i.e., due to the phenological cycles of vegetation, Pettorelli et al. 2006), or as a consequence of human activities (e.g., agriculture and forest management practices; Lande et al. 2014). Hence, large herbivores must continually adjust their use of habitat to these changes. Although relatively overlooked in analytical approaches so far, the order in which habitats are used can be considered as a behavioural tactic to meet different resource needs and cope with other constraints, such as the avoidance of human disturbance and predators, at various spatio-temporal scales (De Goeve et al. 2016, 2020a).

Temporal variation in alternation between open and closed habitats might be due to a complementary functional use of habitats encompassed within the home range (Dunnings 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 (Aikens et al. 2020), instead, they maximized the 'greenness' quality of their ranges. Alternating between habitats could be a tactic to achieve such maximization locally, accessing complementary resources in different habitats (see also Peters et al. 2016).

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 provides thermal protection, shallower snow (Mysterud et al. 1997, Mysterud and Østbye 2006, Ratikainen et al. 2007; Ossi et al. 2015), and potentially better food availability compared to open habitats (Ewald et al. 2014). 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 in winter for 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. This pattern has not been observed in Southern France (FR8), a landscape also consisting of patches of forest within an agricultural matrix. This could be due to the use by deer of small shrubby vegetation patches, typical of Mediterranean environments, that are not defined as forest by TCD (<https://land.copernicus.eu/user-corner/technical-library/hrl-forest>).

To better evaluate these explanations, future studies should look into fine-scale alternation of individuals between habitat types with different vegetation phenology and productivity (see Couriot et al. 2018), while explicitly accounting for the availability of anthropogenic subsidies and resources (Ossi et al. 2016, Ranc et al. 2020a). In this paper, we used a high resolution (20m), but static and simplified, classification of habitats. 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 linked to the resources they offer, revealing their functional role at different spatio-temporal scales (Mandelik et al. 2012; Couriot et al. 2018).

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 the reproductive season (including the birth and territorial seasons). In mammals, males and females have very different schedules of resource allocation to reproduction linked to the species' life history. In roe deer, males are territorial from March until the rut in July-August (Sempéré et al. 1998), while females

mostly give birth in May or June, allocating heavily to late gestation and early lactation during summer. Alternation between open and closed habitats decreased in females during the birth season and the period of intensive maternal care, possibly because of spatial constraints imposed by lactating and avoiding revealing the location of their vulnerable fawn offspring. In contrast, males maintained a higher degree of habitat alternation throughout the summer, possibly linked to territory patrolling and defence (Linnell and Andersen 1998). The fact that these sex-specific patterns were observed in adults, but not fawns, provides further support for these interpretations linked to sex-specific schedules of allocation to reproduction.

Large herbivores' fitness shall depend on the use, or, as we suggest here, alternation, between habitats that are rich enough to ensure the necessary energy intake, but are also safe to provide protection against predators and human disturbance (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 (Mysterud and Østbye 1999), to rumination cycles, where the use of cover is higher during rumination than during feeding bouts (Cederlund 1981), and to repeated visits to the same resource patch, as a result of perception and memory of food availability (Owen-Smith and Martin 2015; Ranc et al. 2021). 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 traits.

Conclusion

Understanding the complexity of animal habitat use and resource requirements is important as it affects a range of ecosystem processes. The frequent alternation between habitats documented here likely affects transportation of seeds, parasites and nutrients between cultivated and more natural habitats. Further, such habitat alternation may affect various other aspects relevant for management, from harvesting efficiency and forest damage, to risk of deer-vehicle collisions. European ecosystems hold fast dynamics due to land use and climate change, and understanding mechanisms and patterns of animal habitat use may help anticipate and mitigate the effects of such changes.

Declarations

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Ethics approval: roe deer captures and collaring were compliant to national and international welfare regulations, and approved as follows. For 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 fulfills their ethical requirements for research on wild animals (Reference number 55.2-1-54-2531-82-10); IT1 and 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 (3B): The animal capture and handling protocols were authorized by the cantonal veterinary and animal welfare services with permit number BE75/11; FR8: prefectoral 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; DE15: The animal capture and handling protocols were authorized by the animal welfare and hunting administration of the federal state of Baden-Wuerttemberg, Germany (RP Freiburg; G-09/53).

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from the EURODEER spatial data base hosted by the Fondazione Edmund Mach (<https://euromammals.org>) and can be accessed upon login. The sub-set of the data and scripts used in the current analysis will be made available on Zenodo upon acceptance.

Authors' contributions: JDG conducted the research with an equal contribution and conceived the study idea and the study design together with FC and NVdW. NM, NCB, MAJH, 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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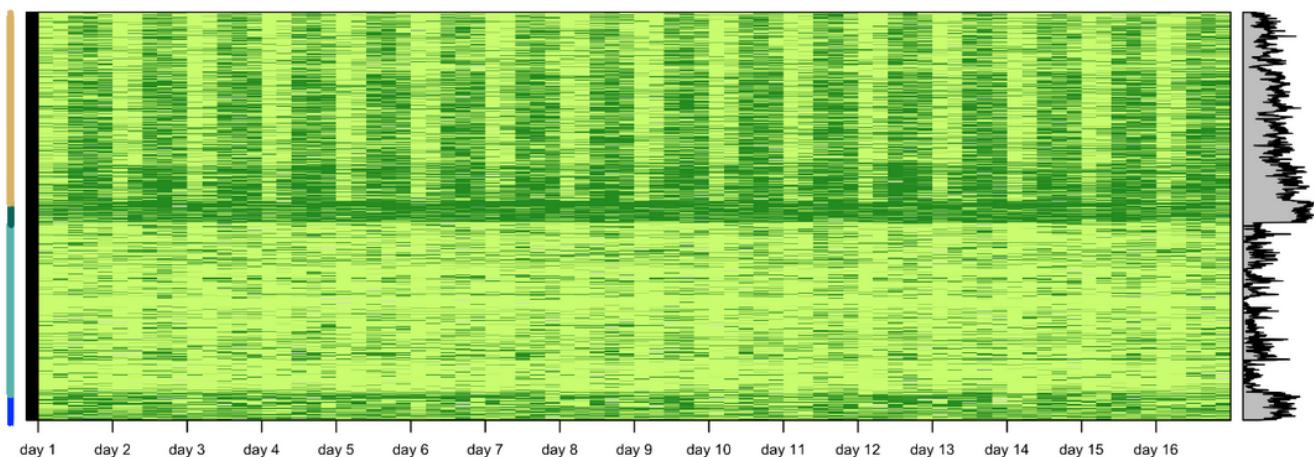
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Figures

Population CH25



Population IT1

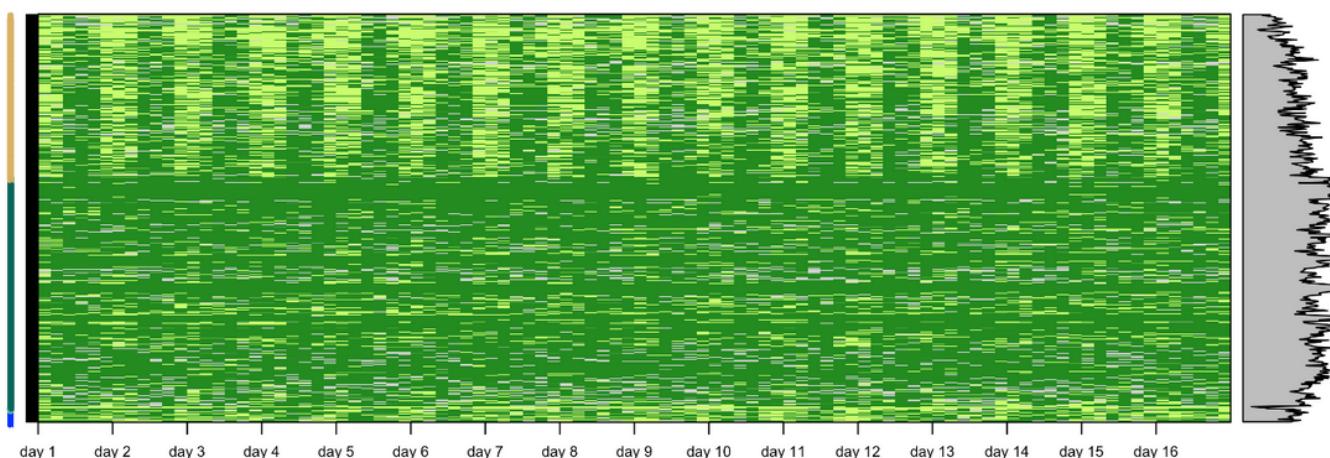


Figure 1

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 animals 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.

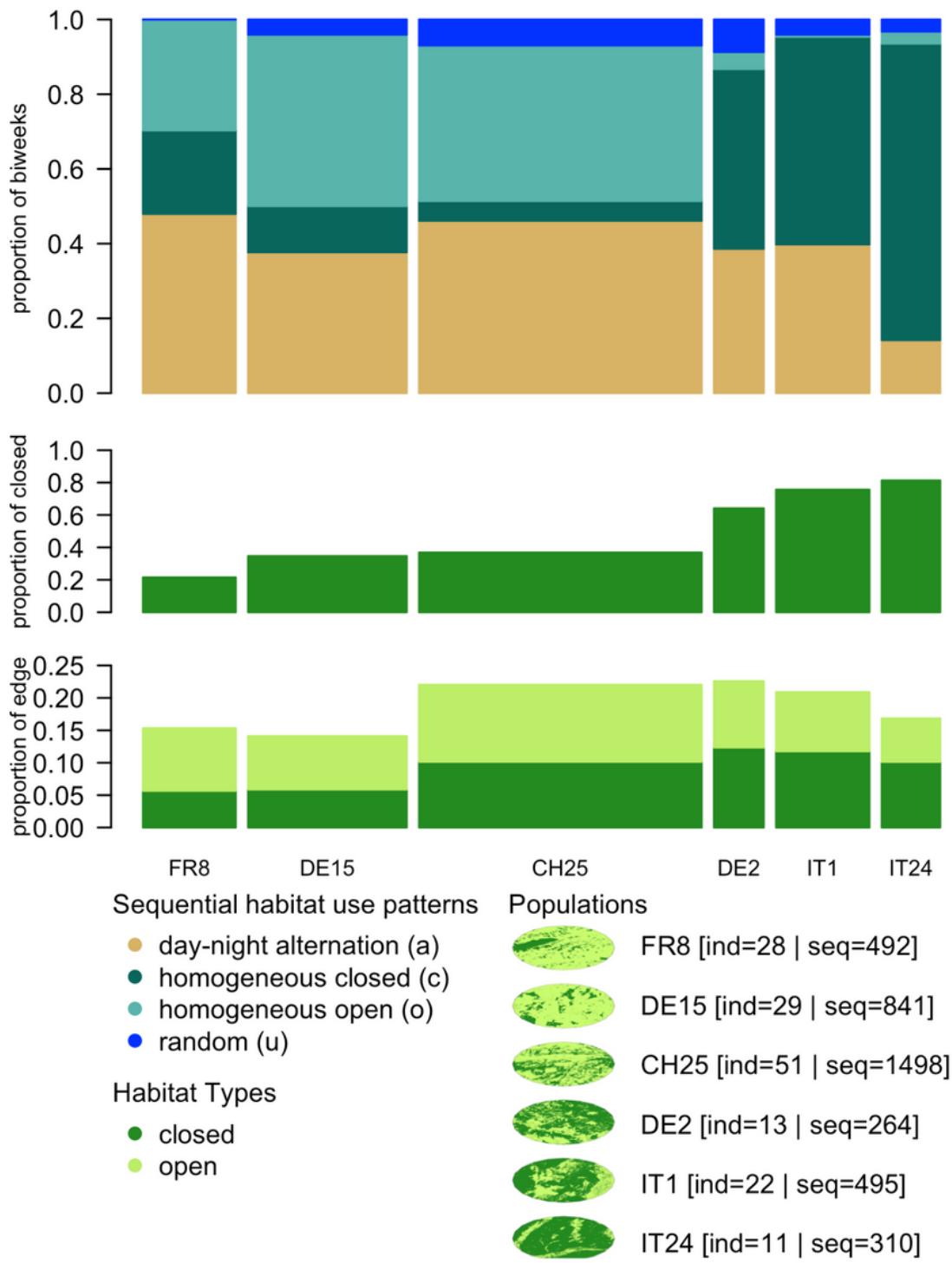


Figure 2

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).

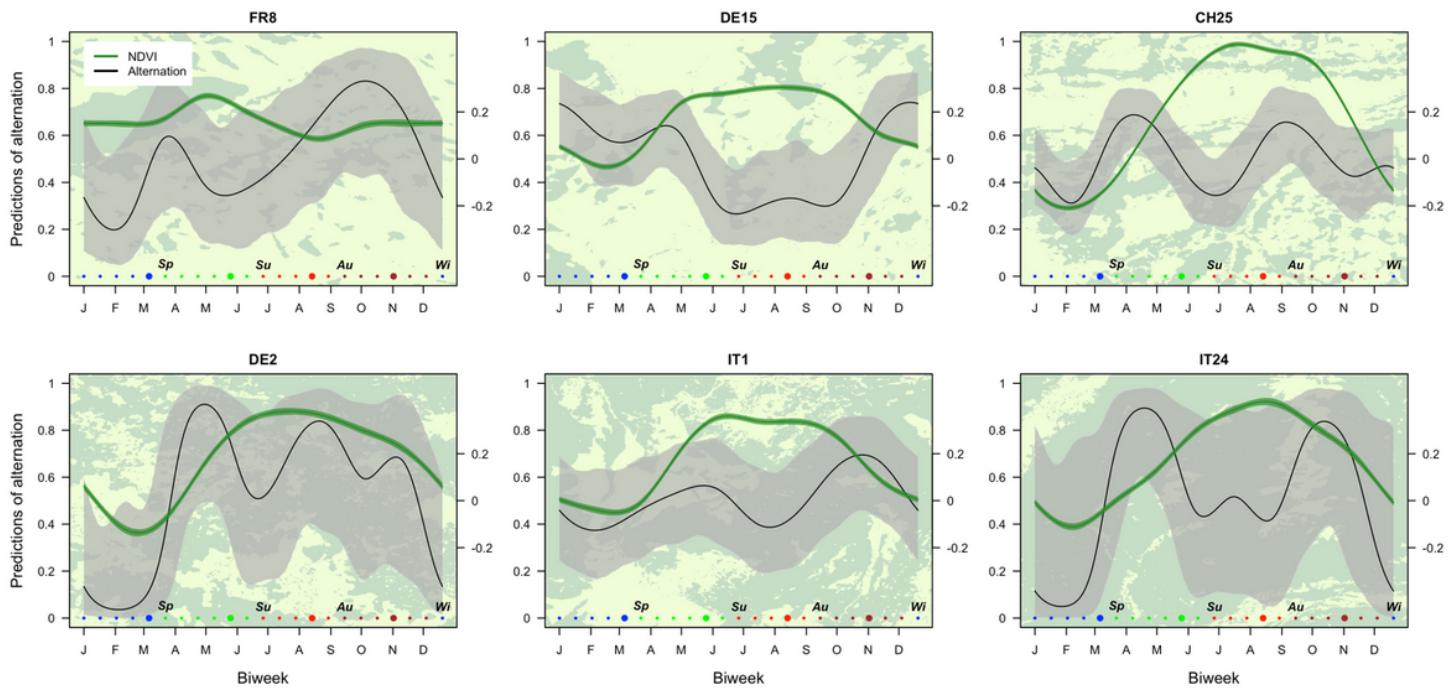


Figure 3

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; green: spring; red: summer; brown: autumn; blue: winter; 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.

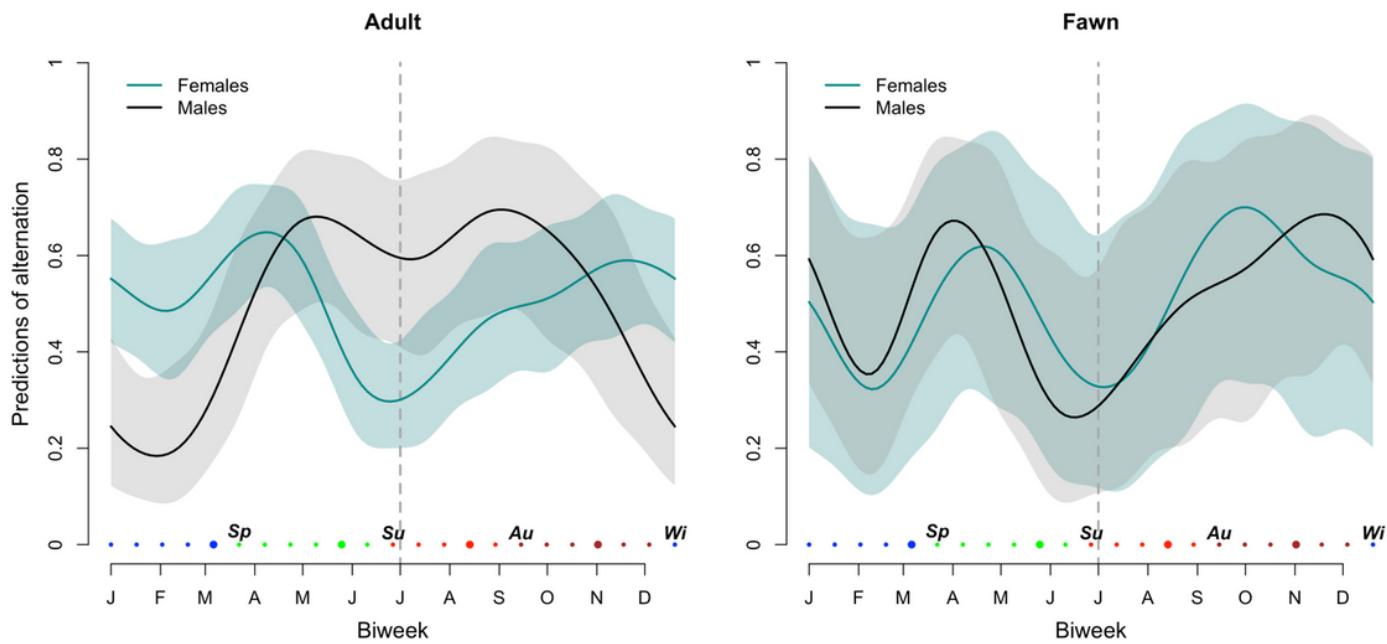


Figure 4

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 Figure 3. The first of July is highlighted by a dashed grey line.

Supplementary Files

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- [Appendix.docx](#)