Modelluntersuchungen zum Wildtiermanagement in Schutzgebieten am Beispiel des Nationalparks Bayerischer Wald

Abschlussbericht

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1 Zusammenfassung

Laut Definition der IUCN (Internationale Union for Conservation of Nature) sind Nationalparke „zur Sicherung großräumiger ökologischer Prozesse ausgewiesene, großflächige, natürliche oder naturnahe Gebiete oder Landschaften samt ihrer typischen Arten- und Ökosystemausstattung“. Für den Umgang mit großen Wildtieren machen diese Richtlinien keine konkreten Angaben und auch in der Bundesdeutschen Gesetzgebung finden sich keine klaren Vorgaben. Erschwerend kommt in Mitteleuropa hinzu, dass Nationalparke in formals genutzten Landschaften ausgewiesen wurden und eine geringe Flächengröße aufweisen. Rahmenbedingungen, die es schwierig machen, das Prinzip „Natur, Natur sein lassen“ im Wildtiermanagement umzusetzen.

Ziel dieses Projektes war es deshalb, Empfehlungen für den Umgang mit Wildtieren im Nationalpark Bayerischer Wald und vergleichbaren Nationalparken in Mitteleuropa zu erarbeiten. Dazu wurde die historische Entwicklung des Wildtiermanagements im Nationalpark Bayerischer Wald und Forschungsfragen zum Verhalten von Rehen und Rothirschen und deren Einfluss auf die Waldentwicklung mit statistischen und individuenbasierten Modellen untersucht.

Die Analysen zur Verteilung des Verbissdrucks im Nationalpark Bayerischer Wald zeigen einen starken Einfluss des Nationalparkmanagements auf die Verteilung des Huftierverbisses, die der Nationalparkzielsetzung einer möglichst wenig vom Menschen gesteuerten Entwicklung entgegenlaufen. Auch die Simulationen zur Waldentwicklung in den nächsten 100 bzw. 1000 Jahren, bei der Szenarien mit unterschiedlichem Verbissdruck und Klimaentwicklung vergleichen wurden, stellen die Sinnhaftigkeit von Managementmaßnahmen in Frage. Es zeigte sich, dass eine Senkung des Verbisses im Vergleich zu den Auswirkungen der prognostizierten Klimaveränderung nur einen sehr geringen Effekt auf die Waldentwicklung hat. Aufgrund von Simulationen mit Hilfe eines individuenbasierten Modells konnte der Einfluss verschiedener Varianten einer früheren Öffnung der Wintergatter untersucht werden. Als Ergebnis kann ein solches Vorhaben nur dann konfliktarm durchgeführt werden, wenn die Fütterung im Wintergatter weitergeführt. Bei den anderen Varianten besteht die Gefahr, dass die Tiere in das Vorfeld des Nationalparks abwandern. Der Öffnungszeitpunkt spielt hingegen nur eine untergeordnete Rolle. Auf Basis dieser Ergebnisse wurde ein Experiment durchgeführt, bei dem zwei Gatter früher geöffnet wurden. Die Beobachtung von besendertern Tieren zeigte, dass hierdurch keine erhörten Schäden im Umfeld des Nationalparks entstanden. Dies in Kombination mit den Ergebnissen der Analyse von Aktivitätsdaten der Tiere, die zeigen, dass die Rothirsche bereits im April eine höhere Aktivität haben, legt den

Schluss nahe, dass eine frühere Öffnung der Wintergatter auch aus Sicht des Tierschutzes geboten erscheint.
Um dem Ziel einer weitgehend vom Menschen unbeeinflussten Entwicklung näher zu kommen, können auf Basis der Projektergebnisse die folgenden Empfehlungen für Nationalparke mit ähnlichen ökologischen Bedingungen (saisonale Lebensräume) gegeben werden, um die Intensität des Wildtiermanagements zu senken.

1. Ein Zeitraum von 20 Jahren reicht aus, um Huftierbestände auf eine Dichte zu senken, die eine Verjüngung der Hauptbaumarten ermöglicht. Anschließend kann die Intensität des Managements zurückgeführt werden, so dass nach dem Übergangszeitraum von 30 Jahren das Ziel, auf 75% der Nationalparkfläche kein Wildtiermanagement zu betreiben, erreicht werden kann.

2 Die Wildtierkontrolle soll zeitlich und räumlich stark beschränkt stattfinden. Der Einsatz von effektiven Methoden, wie beispielsweise Saufängen und Gatterabschüssen, ist dafür notwendig.

2. Fütterungen und Kirrungen sollen auf dem gesamten Nationalparkgebiet nicht eingesetzt werden.

4. Die Rückkehr von großen Beutegreifern, wie Luchs und Wolf, ist eine wichtige Voraussetzung für die Entwicklung einer natürlichen Dynamik und sollte von den Nationalparkverwaltungen aktiv durch Bildungs- und Akzeptanzarbeit unterstützt werden.

2 Anlass und Zielsetzung:

Die in den Vereinigten Staaten von Amerika geborene Nationalparkidee, die sich dem Schutz vom Menschen unberührter Naturlandschaften widmet, gelangte erst mit Verzögerung nach Europa. Die ersten Nationalparke auf dem alten Kontinent wurden 1909 in Schweden (SAREK-Nationalpark) und 1914 in der Schweiz (Schweizerischer Nationalpark) gegründet, jeweils in dünn besiedelten, ursprünglichen, großräumigen Landschaften. Grundidee der Nationalparke ist die Sicherung natürlicher Entwicklungen, ohne Eingreifen des Menschen, unter Einschluss der heimischen Artenausstattung.

Um eine weltweit einheitliche Nomenklatur und Qualitätssicherung von Schutzgebieten zu erreichen, hat die IUCN (International Union for Conservation of Nature) deren Ziele und Aufgaben definiert. Dabei werden sechs verschiedene Schutzgebietstypen unterschieden, die vom Wildnisgebiet bis zu einem Gebiet mit nachhaltiger Ressourcennutzung reichen. Laut dieser Definition sind Schutzgebiete der Kategorie II also Nationalparke „zur Sicherung großräumiger ökologischer Prozesse ausgewiesene, großflächige natürliche oder naturnahe Gebiete oder Landschaften samt ihrer typischen Arten- und Ökosystemausstattung“. Für den Umgang mit Wildtieren machen diese Richtlinien jedoch keine konkreten Angaben, so dass die allgemeinen Leitlinien für die Kategorie II auch auf den Schutz der Wildtiere übertragen werden müssen. Wichtig ist hierbei vor allem die 75%-Regel, die aussagt, dass das vorrangige Ziel der jeweiligen Schutzgebietskategorie für mindestens drei Viertel der Fläche Geltung haben soll, bei Nationalparken entspricht dies eingriffsfreien Flächen.

Konkrete Vorstellungen für den Umgang mit Wildtieren wurden in den nordamerikanischen Nationalparken entwickelt. Dabei zeigte das Wildtiermanagement dort eine lange und kontroverse Entwicklung, die mit der Gründung des Yellowstone Nationalparks 1872 begann. Zunächst wurden die Huftiere vor starker Bejagung und Wilderei geschützt und die Großen Beutegreifer ausgerottet. Dadurch erholten sich die Huftierbestände seit Ende des 18. Jahrhunderts und begannen immer schneller anzusteigen. Mit dem sogenannten Leopold Report wurde Mitte der 1960er Jahre ein erstes Konzept erstellt, das in den Folgejahren eine Leitlinie für das Handeln der Nationalparkverwaltungen bilden sollte. Darin waren beispielsweise auch Maßnahmen zur Kontrolle der Huftierbestände vorgesehen, falls die natürlichen Beutegreifer nicht mehr im jeweiligen Park vorkommen. Das Management der amerikanischen Nationalparke ist heute durch die „Management Policies 2006“ geregelt. Ein umfangreiches Regelwerk, das die Richtschnur für das Management aller US-Nationalparke bildet. Leitbild ist die Aussage: “The National Park Service preserves unimpaired the natural and cultural resources and values of the national park system for the enjoyment, education, and inspiration of this and future generations”. Für das Wildtiermanagement bedeutet das, dass Maßnahmen zur Bestandesregulation grundsätzlich nicht innerhalb der Parke stattfinden. Durch flankierende Maßnahmen wie der Wiederansieldung von Wölfen im Yellowstone Nationalpark, versucht man die Selbsregulierungskräfte von Ökosystemen wiederherzustellen.

Im Gegensatz dazu ist die Situation in Europa sehr uneinheitlich. Es gibt keine europarechtliche Definition für Nationalparke und auch keine Managementgrudsätze. Demzufolge können alle Nationalstaaten diesen Schutzgebietstyp nach eigenen Vorstellungen definieren und machen davon auch Gebrauch. Beispielsweise in Dänemark und Großbritannien entsprechen die Nationalparke eher geschützten Landschaften (Kategorie V) mit Land-, Forst- und Jagdwirtschaft, als Nationalparken der Definition für Kategorie II der IUCN. Entsprechend sind die Spielarten des Wildtiermanagements in europäischen Nationalparken sehr vielfältig und aufgrund der durch Nutzung geprägten Traditionen meist noch stark durch jagd- und forstliche Konzepte beienflusst.

Erschwerend kommt hinzu, dass im Vergleich zu anderen Kontinenten die Anwendung des Nationalparkkonzeptes in Europa auf große Probleme stößt. Während in anderen Kontinenten, vor allem Gebiete die nur wenig vom Menschen beeinflusst sind als Nationalparke ausgewiesen wurden und werden, stehen in den europäischen Landschaften mit ihrer sehr langen Nutzungsgeschichte solche Gebiete nicht mehr zur Verfügung. Die Ausweisung von Nationalparken mit dem Ziel Areale in einem nicht vom Menschen beeinträchtigten (unimpaired) Zustand zu erhalten, wie es in z.B. in Nordamerika vorgesehen ist, kann in Europa deshalb nicht umgesetzt werden. Um dieses Dilemma aufzulösen, wurde das Konstrukt eines Entwicklungsnationalparks geschafften und im Bundesnaturschutzgesetz verankert. Auf dieser Basis können nun Nationalparke auch in der stark vom Menschen veränderten Landschaft Europas ausgewiesen werden. Diese Gebiete sollen nach ihrer Ausweisung als Nationalpark in einem maximal 30 jährigen Übergangszeitraum so weiterentwickelt werden, dass sie anschließend die Anforderungen an einen Nationalpark gemäß IUCN-Richtlinien erfüllen.

Darüber hinaus verfügen Nationalparke in Deutschland meist über Rahmenbedingungen, die es schwierig machen, das Prinzip „Natur, Natur sein lassen“ im Wildtiermanagement umzusetzen. Im Nationalpark Bayerischer Wald, der hier als Beispiel für andere Nationalparke dient, sind dies vor allem:

1. Die Wälder des Nationalparkgebietes wurden in den letzten Jahrhunderten stark durch deren Bewirtschaftung verändert. Aus den ursprünglichen Buchen-Tannenwäldern entstanden Fichten-Buchen-Wälder. Der Anteil der Fichte

stieg dabei von etwa 30 % zu Beginn der geregelten Bewirtschaftung auf über 70% an, während der Anteil der Tanne im gleichen Zeitraum von etwa 30 % auf unter 3% zurückging. Gleichzeitig wurden die struktur- und vorratsreichen Bergmischwaldbestände in Altersklassenwald umgewandelt.

2. Die Großprädatoren Wolf und Bär sind im Gebiet ausgerottet. Aufgrund dieser Situation können wesentliche natürliche Regulationsmechanismen für die Rothirschpopulation nicht mehr greifen. Bei den Rehen ist die Situation günstiger, da der Luchs als wichtiger Prädator seit Anfang der 90er Jahre wieder regelmäßig im Nationalparkgebiet vorkommt.
3. Die großen noch rezenten Pflanzenfresser Wisent und Elch kommen auf dem Nationalparkgebiet nicht mehr vor. Damit können interspezifische Konkurrenzmechanismen und damit ggf. einhergehende Verdrängungsmechanismen nicht mehr greifen.
4. Aufgrund der kleinen Fläche des Schutzgebietes können natürlich stattfindende populationsdynamische Prozesse der Huftierpopulationen nicht innerhalb der Grenzen des Nationalparks ablaufen. Damit haben starke Bestandesfluktuationen immer auch Auswirkungen auf das Umfeld des Schutzgebietes. Zusätzlich umfasst der Nationalpark vor allem die Sommerlebensräume der Huftiere. Unter naturnahen Bedingungen würde ein Teil der Rothirsche aufgrund der hohen Schneelage den Nationalpark im Winter verlassen und tiefer gelegene Gebiete aufsuchen. Darüber hinaus reichen die individuellen Streifgebiete von Rehen und Rothirschen zum Teil weit über die Nationalparkgrenzen hinaus. Damit ist der Nationalpark kein isoliertes System, vielmehr stehen die Huftiere in unmittelbarer Wechselwirkung mit dem Umfeld und den Enklaven im Nationalparkgebiet. Verbiss und Schäle werden dort auf den wirtschaftlich genutzten Grundstücken als Schäden angesehen und müssen in engen Grenzen gehalten werden.

Ziel des Wildtiermanagements muss es sein, auf Basis von Forschungsergebnissen unter den gegebenen Rahmenbedingungen einen Ausgleich zwischen den Interessen des Prozesschutzes (möglichst keine Eingriffe) und der an den Nationalpark angrenzenden Landwirte, Waldbesitzer und Jäger (möglichst geringe Schäden) herzustellen. Dabei müssen übergeordnete Aspekte der menschlichen Gesundheit (Tierseuchen) berücksichtigt werden. Dieses durch die Deutsche Bundesstiftung Umwelt geförderte Projekt soll naturwissenschaftliche Grundlagen für ein nationalparkgerechtes Wildtiermanagement erarbeiten und daraus Empfehlungen für den Nationalpark Bayerischer Wald und ökologisch vergleichbare Nationalparke Mitteleuropas ableiten.

3. Geschichtliche Entwicklung des Wildtiermanagements im Nationalpark Bayerischer Wald

Ziel dieses Abschnittes ist es, die Entwicklung des Schalenwildmanagements in 40 Jahren Nationalparkgeschichte zu rekonstruieren. Es soll die Frage beantwortetet werden, welche Leitbilder, Grundsätze und Motivationen es für das Schalenwildmanagement gab und wie diese auf der Fläche umgesetzt wurden. Zur Rekonstruktion der Geschichte des Wildtiermanagements wurden drei Methoden eingesetzt: Literaturstudie, Experteninterviews und die zahlenmäßige Analyse der Abschussmeldungen. Dabei wurden drei Perioden unterschieden.

Wildtiermanagement 1970-1985

Die Zuständigkeit für Jagdfragen wurde 1970 dem neu gegründeten Nationalparkamt übertragen, dessen erklärtes Ziel war in den Anfangsjahren die Reduzierung der künstlich überhöhten Wildbestände, um Verbiss und Schäle zu verringern. Man strebte eine Anpassung an die natürliche Lebensraumkapazität an – Weiser war die Entwicklung der Verjüngung. Dafür wurden Rothirsche und Rehe auf der gesamten Fläche des Nationalparks und innerhalb der gesetzlichen Jagdzeiten aufs intensivste bejagt. Trophäenjagd und Hege wurden eingestellt und der Begriff Wildbestandsregulierung eingeführt. Die freien Fütterungen löste die Nationalparkverwaltung bis Mitte der 1980er Jahre Stück für Stück auf und errichtete zur Überwinterung des Rotwildes Anfang der 1970er Jahre drei Wintergatter.

Wildtiermanagement 1986-1997

Auf die Reduzierungswelle und die Umbruchzeit der Anfangsjahre folgte in der Periode 1986-1997 eine Phase der Stabilisierung. Der Verbiss von Bodenflora und Baumverjüngung war in dieser Periode noch immer der Hauptgrund für die Bestandeskontrolle. Die Eingriffe wurden jetzt auch unter dem Gesichtspunkt der Störung der Tiere beurteilt. Deshalb wurden die Abschüsse seit 1987 zeitlich und örtlich beschränkt. So hat man die Jagdzeit auf den Zeitraum vom 01.09. bis zum 31.01. verkürzt und im Kerngebiet jagdliche Aktivitäten unterbunden. Des Weiteren hat man vermehrt Drückjagden auf Rotwild organisiert und zudem war es ab 1986 mit jährlicher Genehmigung möglich, die Rothirsche auch im Wintergatter zu regulieren. Eine dauerhafte Legalisierung des Gatterabschusses brachte ein Passus in der 1992 erlassenen Nationalparkverordnung mit sich. Als dritte Schalenwildart hat sich seit Mitte der 1980er Jahre das Wildschwein im Nationalpark etabliert und sorgte nach einem kräftigen Anstieg der Population bereits Ende jenes Jahrzehnts für Schäden an Privatgrundstücken in den Ortschaften, die vom Nationalpark umschlossen sind. Aus diesem Grund begann man, das Schwarzwild mit Hilfe von Saufängen zu regulieren.

Wildtiermanagement 1997 bis 2012

Die letzte Periode des Schalenwildmanagements wurde besonders von veränderten Rahmenbedingungen beeinflusst: Der Nationalpark wurde erweitert, der Prozessschutz gesetzlich verankert, die Borkenkäfervermehrung ist fortgeschritten und es hat sich eine Luchspopulation etabliert. Seit 2011 gibt es zudem einen offiziell festgesetzten Nationalparkplan, in welchem u.a. auch die Ziele und Leitbilder für das Schalenwildmanagement formuliert sind. Vorrangig ist die Erhaltung der heimischen Schalenwildarten zu nennen, neben vielen weiteren Zielen, wie dem Erhalt der Biodiversität, Verringerung des selektiven Verbisses im Randbereich, Sichtbarkeit, Schadensvermeidung, Minimierung der regulativen Eingriffe und Abstimmung mit dem Nationalpark Šumava. Mit Erweiterung des Parks hat man die Drückjagden eingestellt. Bezüglich des Rotwildmanagements besteht v.a. im Altgebiet eine starke Bindung an das Wintergatter – die Gatterbestände sollen kontrollierbar bleiben, deshalb gibt es dort die Tendenz, den Rotwildbestand leicht zu reduzieren. Das von der Nationalparkverwaltung initiierte Projekt „Rothirsch auf neuen Wegen“, das das Ziel eines großflächig, besser abgestimmten Rothirschmanagements und die Auflassung der Wintergatter verfolgte, wurde von den Vertretern der Jäger und Waldbesitzer im Landkreis Regen abgelehnt und kam deshalb nicht zustande. Die Bestandeskontrolle bei den Rehen hat die Nationalparkverwaltung stetig reduziert und seit 2007 den Rehwildabschuss im Altgebiet und seit 2012 den Abschuss im Gesamtgebiet eingestellt. Kriterium für den Eingriff in die Wildschweinbestände ist die Schadensintensität an den landwirtschaftlich genutzten Flächen der Enklaven. Treten Schäden auf kommen innerhalb des Zeitraums vom 16.06. bis 31.01. an den Schadensschwerpunkten Saufänge zum Einsatz

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht (Anlage 1):

Heurich M. und K. Engelhardt: Entwicklung des Huftiermanagements im Nationalpark Bayerischer Wald. Der lange Weg zum nationalparkgerechten Umgang mit Huftieren.

4 Bewegungs- und Waldnutzungsmuster der Rehe und Rothirsche im Nationalpark Bayerischer Wald

4.1 Statistische Analyse von Einflussgrößen auf die Verbissintensität auf Landschaftsebene

Nationalparke blicken in Europa meist auf eine relativ kurze Geschichte zurück und wurden, bis auf wenige Ausnahmen, in formals genutzten Landschaften ausgewiesen. Es handelt sich also um sogenannte Entwicklungsnationalparke. Auch die Wälder der heutigen Nationalparke wurden intensiv genutzt, die Huftierbestände gehegt und die großen Beutegreifer ausgerottet. Nun besteht die Aufgabe der Nationalparkverwaltungen unter diesen Voraussetzungen, die ursprünglichen Artenzusammensetzungen und Prozesse zu entwickeln und zu schützen. Dabei stellt sich die Frage, mit welchen Managementmethoden diese Ziele erreicht werden können. Dafür ist es von großer Bedeutung, dass das Management die verfolgten Ziele nicht negativ beeinflusst. Um hier Aussagen treffen zu können, müssen die Effekte des Managements von den biotischen und abiotischen Einflüssen isoliert werden. Um die Hypothese zu testen, dass der Verbiss vor allem durch Umweltvariablen beeinflusst wird, wurden die Daten über den Verbiss an der Waldverjüngung von 5800 Inventurpunkten im Nationalpark Bayerischer Wald ausgewertet. Dabei zeigte sich, dass die Verbissintensität die Verjüngung von Weißtanne, Vogelbeere und Buche erlaubt. Mit Hilfe von räumlich additiven logistischen Regressionsmodellen konnte durch den Vergleich verschiedener Variablensets der Bereiche Bodenvegetation, Verjüngung, Topographie, Altbestand und Management gezeigt werden, dass die Managementaktivitäten und der Raum den größten Beitrag zur Erklärung der Variation des Verbissdrucks leisten. Diese Ergebnisse unterstreichen, dass die Nationalparkverwaltung mit ihren Aktivitäten erheblich zur Variation des Verbissdrucks im Gelände beiträgt und damit ihre eigenen Ziele, nämlich den Einfluss anthropogener Einflüsse auf das System zu reduzieren, konterkariert. Insbesondere die Wintergatter, die Zone mit Wildtiermanagement und die den Park durchziehenden Wanderwege erweisen sich als nachteilig für den Schutz möglichst ungelenkter Prozesse. Deshalb sollten alle Parkverwaltungen genau überprüfen, welche Einflüsse ihre Managementaktivitäten auf die Schutzgebiete haben und wo immer angebracht und möglich auf Eingriffe verzichten.

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht (Anlage 2):

Möst, L., Hothorn T., Müller, J. and Heurich M. (2013): How to manage ungulates in a national park? Unintended side effects of management measures on the distribution of browsing pressure in the landscape. Submitted to Journal of Environmental Management.

4.2 Statistische Analyse von Einflussgrößen auf die Größe und Lage von Streifgebieten von Rehen und Rothirschen

Das Verständnis der Bewegungsmuster von Tieren ist für eine Weiterentwicklung und Verwirklichung von Naturschutzzielen und –maßnahmen von großer Bedeutung. Streifgebiete verknüpfen die Bewegung von Tieren mit der Verteilung der Ressourcen, die für ihr Überleben und ihre Reproduktion notwendig sind.

Verschiedene Faktoren beeinflussen die Größe von Streifgebieten. Dazu gehören unter anderem die Körpergröße, Geschlecht und Alter, die Verfügbarkeit von Nahrung sowie intra-, interspezifischer Konkurrenz und die Landschaftsbeschaffenheit. Im Rahmen des Projektes wurden diese Ansätze erweitert, in der nicht nur der Anteil verschiedener Habitattypen innerhalb eines Streifgebietes berücksichtigt, sondern zusätzlich die Landschaftskonfiguration, also die räumliche Anordnung von Habitattypen mit in die Analysen einbezogen wurde.

Dazu wurden die Daten von 32 besenderten Rothirschen (14 männlich, 18 weiblich) aus den Jahren 2002–2009 verwendet. Vier Individuen waren über zwei oder mehr Jahre besendert. Für die Rehe stand uns ein Datensatz von 45 Individuen aus den Jahren 2005-2010 zu Verfügung. Die Streifgebietsgröße wurde mit der „fixed kernel“ Methode und der Referenzmethode für den „smoothing factor h“ in der Software R 2.13.2 mit dem Packet „adehabitatHR“ bestimmt. Dabei wurden 50%, 70% und 90% Kernel für drei zeitliche Skalen berechnet: monatlich, zweiwöchentlich und wöchentlich. Um den Einfluss der verschiedenen Landbedeckungen, der klimatischen Variablen und der Landschaftskonfiguration auf die Streifgebietsgröße zu untersuchen, wurde ein lineares gemischtes Modell verwendet.

Die Ergebnisse zeigen, dass vor allem die Landschaftskonfiguration einen hohen Erklärungswert zur Dynamik der Streifgebiete liefert und dass diese Variable auch in Zukunft bei ähnlichen Analysen berücksichtigt werden muss. Der Effekt der Landschaftskonfiguration auf die Größe der Streifgebiete ist bei Rothirschen auf allen räumlichen und zeitlichen Skalen vorhanden und stark ausgeprägt. Mit Zunahme der Aggregation der Landschaftspatches steigt die Größe der Streifgebiete. Bei den Rehen zeigt sich neben einer ausgeprägten Individualität, im Gegensatz zu den Rothirschen, auch ein Unterschied zwischen den Geschlechtern. Bei den Männchen gibt es im Bezug zum Landschaftsindex kein einheitliches Bild, während bei den Weibchen auf allen räumlichen und zeitlichen Skalen ein starker Effekt vorhanden ist. Beim Rothirsch hat zudem die Meereshöhe einen starken Einfluss auf die Streifgebietsgröße, der vor allem durch die nahrungsreichen Fichtenwaldgesellschaften in den Tal- und Hanglagen beeinflusst ist. Der wichtigste Habitattyp zur Erklärung der Homerangegröße bei den Rehen sind die Wiesen. Witterungsparameter liefern hingegen nur einen unbedeutenden Erklärungsbeitrag.

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht (Anlage 3):

Bevanda, B., Fronhofer, E.A., Heurich, M. and Reineking B. What determines home range size? The importance of a landscape's spatial configuration.

4.3 Analyse der Habitatnutzung von Rehen und Rothirschen innerhalb ihrer Streifgebiete

Warum Tiere bestimmte Habitate häufiger nutzen als andere ist eine fundamentale Frage der Tierökologie. Im Wesentlichen handelt es sich bei der Habitatnutzung um einen Optimierungsprozess, bei dem das Individuum zwischen größtmöglicher Nahrungsaufnahme und größtmöglicher Sicherheit abwägen muss. Hält sich das Tier in Habitaten mit größtmöglicher Nahrungsverfügbarkeit auf, die aber beispielsweise nicht viel Deckung bieten, kann es leicht von Feinden getötet werden. Hält es sich in Bereichen auf, wo es sich vor Feinden verbergen kann, muss es mit weniger ergiebigen Nahrungsgründen vorlieb nehmen, was seine Fitness beeinträchtigt.

Um die zeitliche Habitatnutzung von Rehen und Rothirschen innerhalb ihrer Homeranges zu untersuchen, wurden Generalisierte Additive Modelle mit gemischten Effekten zur Analyse der GPS-Daten verwendet. Zur Analyse der Habitatnutzung im Winter wurden Step-Selection-Funcitons eingesetzt. Die Habitatvariablen wurden aus Fernerkundungsdaten abgeleitet. Dabei wurden erstmalig hochaufgelöste Lidardaten in Kombination mit Beschleunigungssenoren für die Analyse der Habitatnutzung eingesetzt.

Die Ergebnisse der Analysen zeigen eine starke Abhängigkeit der Habitatnutzung von Tages- und Jahreszeit. Bei den Rehen gibt es zudem eine sehr hohe individuelle Variabilität der Habitatnutzung. Als Muster zeichnet sich ab, dass Rehe und vor allem Rothirsche nahrungsreiche Wiesen nur nachts nutzen und sich tagsüber in deckungsreichen Habitaten aufhalten. Bei den Rehen sind dies vor allem Verjüngungsflächen und Mischbestände, bei den Rothirschen mittelalte

Nadelbaumbestände (Abb1 und 2). Im Winter wird die Habitatnutzung der Rehe vor allem durch Kirrungen (relative Bedeutung: 0.53) und den Schlussgrad der Bestände (relative Bedeutung: 0.11) bestimmt.

Diese Ergebnisse zeigen deutlich, dass sich Rehe und Rothirsche im Nationalpark am Tag in dichten Beständen aufhalten. Sie verhalten sich also ähnlich wie in Gebieten, in denen Jagd ausgeübt wird. Als Folge sind die Tiere für Nationalparkbesucher nur sehr schwierig beobachtbar. Um die Ursachen für dieses Verhalten der Tiere im Nationalpark besser beurteilen zu können, wäre es notwendig Vergleichsuntersuchungen mit Gebieten unterschiedlicher Bejagungsintensität durchzuführen. Bei der Habitatnutzung im Winter fällt auf, dass das Verhalten der Tiere massiv durch die Gabe von Futter an Kirrungen beeinflusst wird. Um die Prozesse im Nationalpark möglichst wenig zu beeinflussen, sollte deshalb auf eine Ausbringung von Futtermaterial verzichtet werden.

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht:

Anlage 4:

Dupke, C., Reineking, B., Ewald, M., Zeppenfeld, T., Heurich, M.: Resource distribution explains temporal dynamics in habitat use by European roe deer.

Anlage 5

Ewald, M., Claudia Dupke, C., Heurich, M., Müller, J. and Reineking, B.: LiDAR remote sensing and GPS-telemetry data: Gaining precision in winter habitat selection of European roe deer.

Die in diesem Projekt entwickelten Modelle zur Analyse der Streifgebiete und der Analyse der Habitatnutzung innerhalb der Streifgebiete befinden sich als Zipfile in Anlage 10 zu diesem Bericht:

a) Modelle zur Analyse der Streifgebiete.zip

b) Modelle zur Analyse der Habitatnutzung.zip

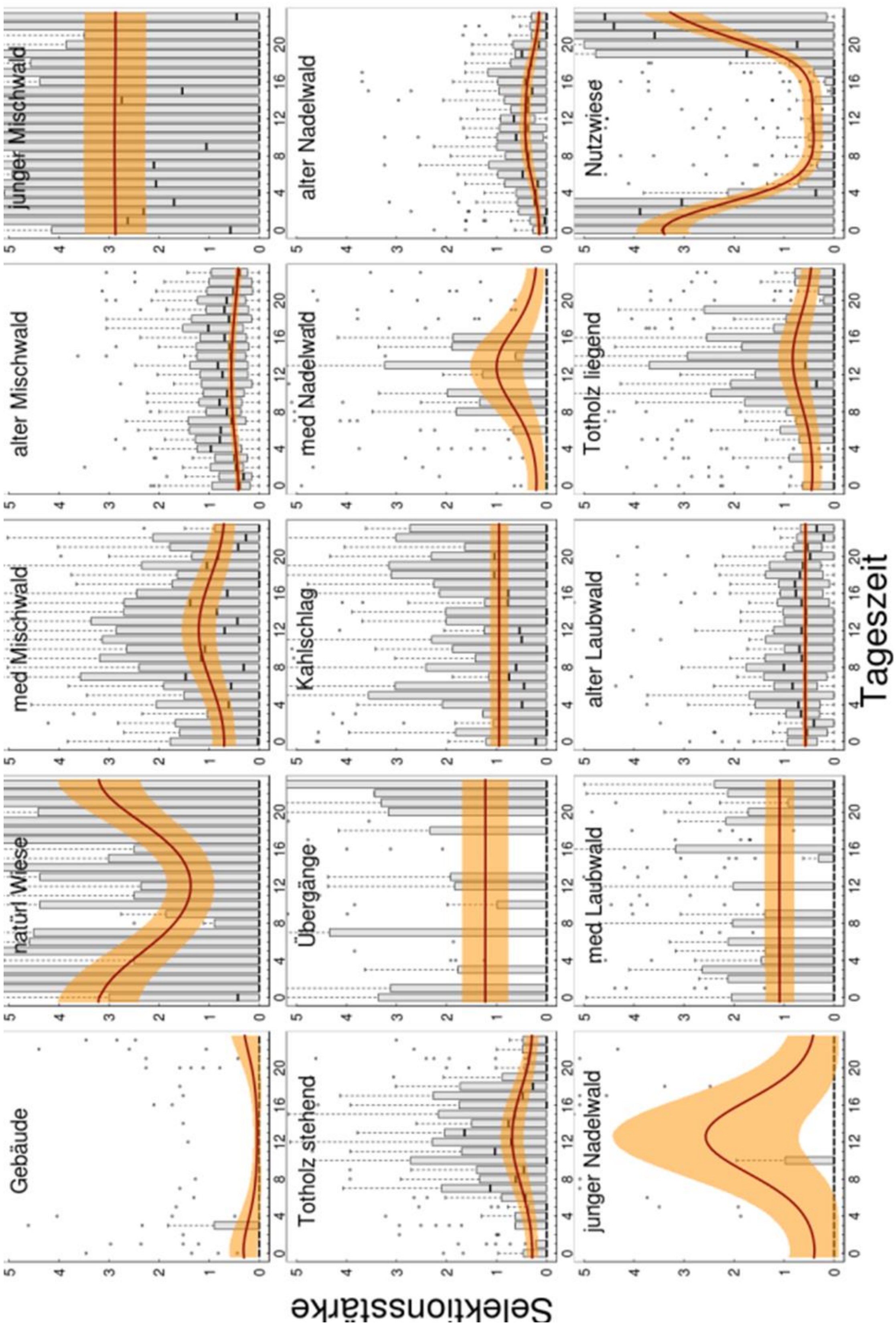

Abb 1: Habitatwahl der Rothirsche in Abhängigkeit von der Tageszeit. Die Boxplots zeigen die Verteilung der Rohdaten. Die rote Line das Ergebnis der Modellierung und die orangene Fläche das Konfidenzband.

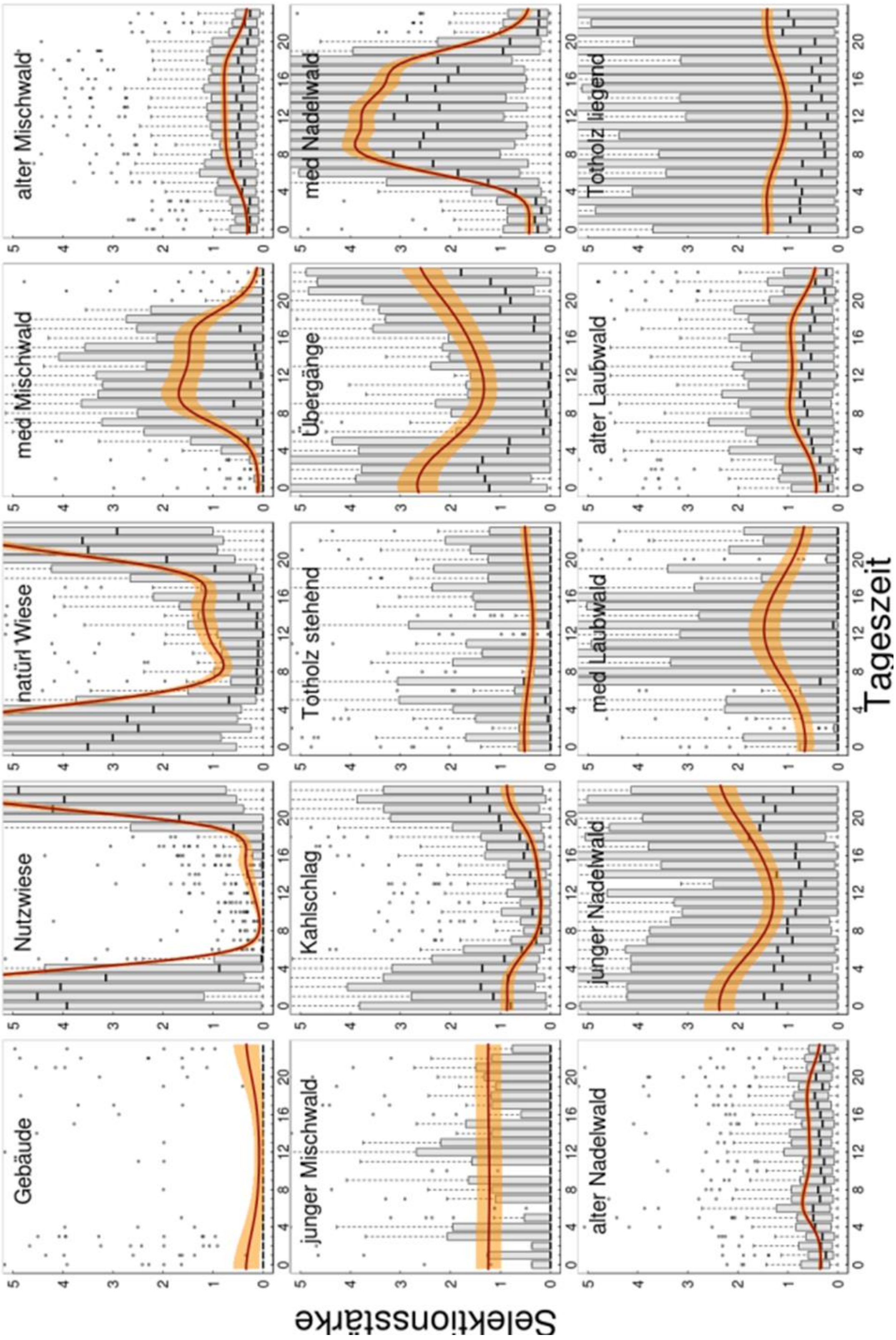

Abb. 2: Habitatwahl der Rothirsche in Abhängigkeit von der Tageszeit. Die Boxplots zeigen die Verteilung der Rohdaten. Die rote Line das Ergebnis der Modellierung und die orangene Fläche das Konfidenzband.

4.4 Analyse der Aktivitätsrhythmik von Rothirschen

Das Aktivitätsverhalten von Tieren wird sowohl von inneren als auch äußeren Faktoren gesteuert. Wichtige Umweltfaktoren sind dabei der Wechsel von Tag und Nacht, sowie die Folge der Jahreszeiten. Die sich daraus ergebenden Aktivitätsrhythmen werden durch weitere Faktoren, wie die Witterung, die Temperatur, die Nahrungsverfügbarkeit und Beutegreifer modifiziert. Zu den inneren Faktoren gehören physiologische Abläufe, wie der Äsungs- und Reproduktionszyklus. Die sich daraus ergebenden Aktivitätsrhythmen der Tiere stellen eine Optimierung der Einzelkomponenten zur Maximierung der Fitness dar.

Ziel dieser Studie ist die Analyse des Aktivitätsverhaltens von Rothirschen im Nationalpark Bayerischer Wald im Tages- und Jahreslauf, um den Einfluss der Wintergatter und der Nichtbejagung auf das Tierverhalten zu untersuchen. Dazu wurden die Daten von Beschleunigungssensoren, die in den Halsbändern von 12 Rothirschen eingebaut waren, verwendet. Diese Sensoren registrieren alle 5 Minuten einen Wert, der die Aktivität der Tiere beschreibt.

Im Jahreslauf findet man die höchste Aktivität der Tiere im Mai und Juni, sowie im September. Die Aktivität in den Wintermonaten ist wesentlich niedriger als im Sommer. Die Aktivität in den Sommermonaten ist in die Nacht verschoben, während insbesondere die Weibchen im Winter ein ausgeglichenes Tag-Nacht-Verhältnis aufweisen. In den Sommermonaten kann ein täglicher Rhythmus mit zwei starken Aktivitätspeaks in der Morgen- und Abenddämmerung gefunden werden, während im Winter der Aktivitätspeak in den Morgenstunden wegfällt. Zusätzlich zum Peak in der Abenddämmerung bildet sich im Winter ein weiterer Aktivitätspeak am Nachmittag heraus.

Trotz einer jagdfreien Zone von 17.000 ha im Nationalparkgebiet kann eine Verschiebung der Aktivität in den Tag, wie sie für nicht bejagte Populationen oft postuliert wird, nicht beobachtet werden. Demgegenüber haben die Wintergatter, wie zu erwarten, einen starken Einfluss auf das Aktivitätsverhalten. In den Aktogrammen zeichnet sich die Periode in den Gattern als ein Zeitraum mit niedriger Aktivität deutlich ab. Zudem führt die Fütterung am Mittag zu einem Rhythmus mit einem sekundären Aktivitätspeak am Nachmittag. Ob der Wegfall des Aktivitätspeaks in den Morgenstunden mit der Haltung im Wintergatter zusammenhängt oder eine Anpassung an kalte Wintertemperaturen darstellt, könnte erst durch einen Vergleich mit Tieren, die außerhalb der Wintergatter überwintern nachgewiesen werden. Wichtig für das Management ist die Beobachtung, dass die Aktivität der hochträchtigen weiblichen Tiere bereits vor der Öffnung der Gatter im April stark ansteigt. Daraus kann die Empfehlung abgeleitet werden, die Gatter bereits Anfang April zu öffnen.

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht:

Anlage 6:

Berger, A., Krop-Benesch, A., Hofer H. and M. Heurich: Seasonal variation in circadian activity patterns in red deer (Cervus elaphus) in Bavarian Forest National Park

4.5 Prozessbasierte Beschreibung der Raumnutzung von Rothirschen durch individuen-basierte Modellierung des Bewegungsverhaltens

Das entwickelte Bewegungsmodell simuliert auf Grundlage von GPS-Daten und Verhaltensregeln Bewegungspfade, die den realen Pfaden hinsichtlich ausgewählter Kriterien sehr ähnlich sind. So simuliert das Modell einen tageszeitlichen Rhythmus, der die Präferenz bzw. Abneigung bezüglich verschiedener Faktoren variieren lässt. Faktoren sind Nahrungsangebot, Deckung, Störungen durch Straßen und Gebäude, sowie die Entfernung zum Streifgebietszentrum und mittlere Schrittweite.

Die Landschaft wird durch ein Gitter aus 50x50 m² Zellen repräsentiert. Jede Gitterzelle erhält auf Grundlage von Lidardaten und Biomassebestimmung einen

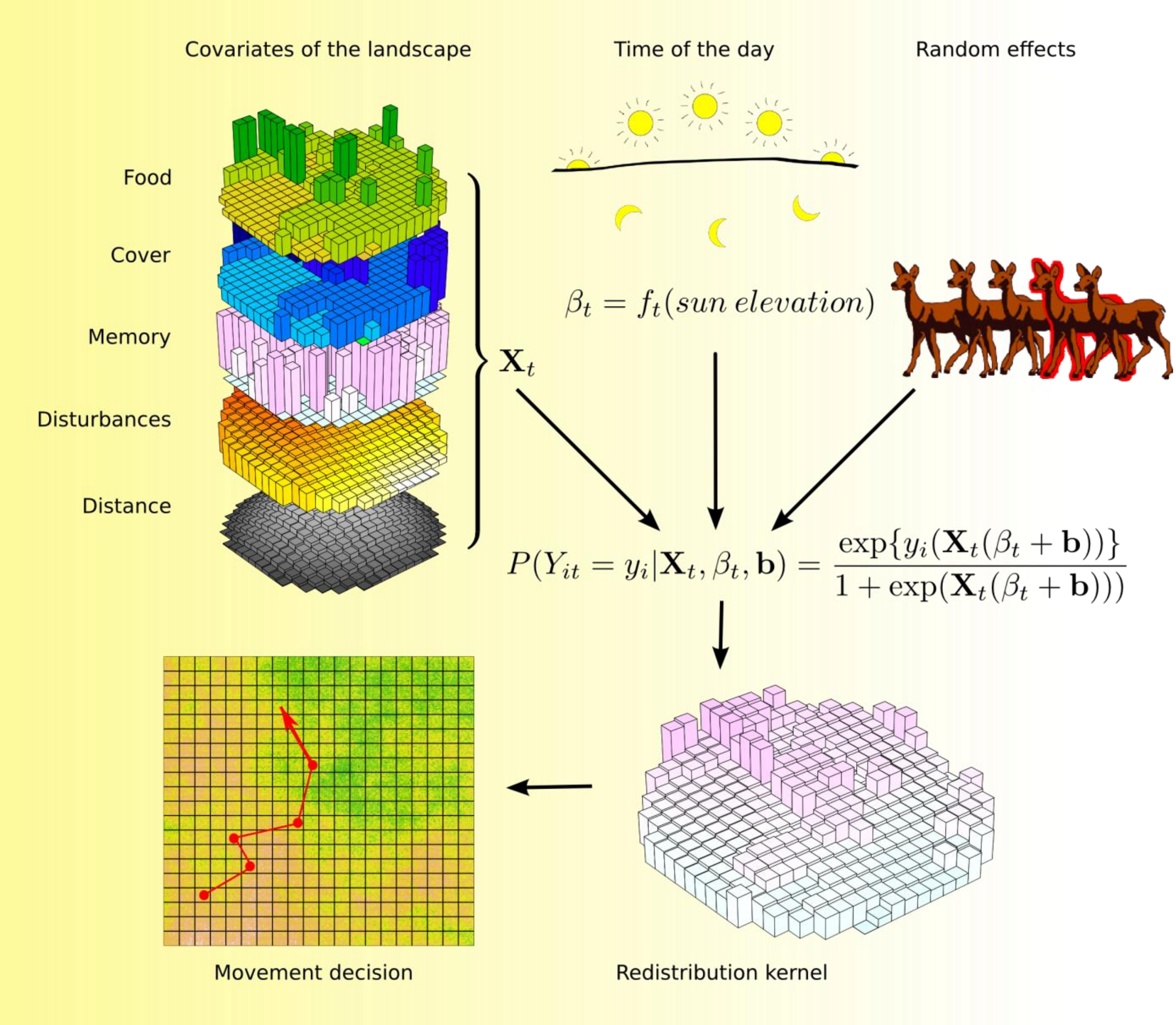

Abbildung 3: Modellübersicht: Informationen aus der Landschaft, die Tageszeit, sowie Informationen zum Individuum fließen in das Modell, das daraus zunächst die Attraktivität für jede Gitterzelle berechnet. Diese ist die Grundlage für eine Bewegungsentscheidung. Die Wiederholungen von Bewegungsentscheidungen liefern simulierte Pfade

Wert für Deckungs- bzw. Nahrungsangebot. Individuen sind charakterisiert durch eine ID, Geschlecht und ein monatliches Streifgebietszentrum. Ein Pfad wird simuliert, indem eine Folge von Bewegungsentscheidungen simuliert wird (Abb. 3). Bewegungsentscheidungen werden auf Grundlage von Wahrscheinlichkeiten zufällig getroffen. Jeder Gitterzelle im Umkreis der derzeitigen Position des Individuums wird eine Wahrscheinlichkeit zugeordnet, welche die derzeitige Attraktivität widerspiegelt. Diese Attraktivität ist abhängig vom Geschlecht des Tieres, sowie der Entfernung zum Streifgebietszentrum, dem Nahrungs- und Deckungsangebot und der Entfernung zu Straßen und Gebäuden. Anziehung bzw. Abstoßung dieser Faktoren variiert über die Tageszeit. In welcher Weise und wie stark Anziehung bzw. Abstoßung der Faktoren wirken, kann auf Grundlage der realen Daten geschätzt werden.

Dafür wurde ein generalisiertes Modell mit gemischten Effekten verwendet (GLMM), wobei auf Grundlage von “Step selection functions” (SSF), Präferenz bezüglich verschiedener Faktoren quantifiziert werden konnte. Um die zeitliche Variation von Präferenz zu gewährleisten, wurde ein nicht-lineares Koeffizienten-variierendes Modell verwendet, wobei zyklische B-splines für die Variation der Koeffizienten über die Zeit sorgen. Heterogenität zwischen den Individuen wird berücksichtigt durch einen gemischten Effekt, der die Koeffizienten auch für einzelne Individuen variieren lässt.

Das Modell wurde evaluiert, in dem Muster in den simulierten Daten, die auf Grundlage der Modellregeln entstanden sind, mit den Mustern in den realen Daten verglichen wurden (Abb.4).

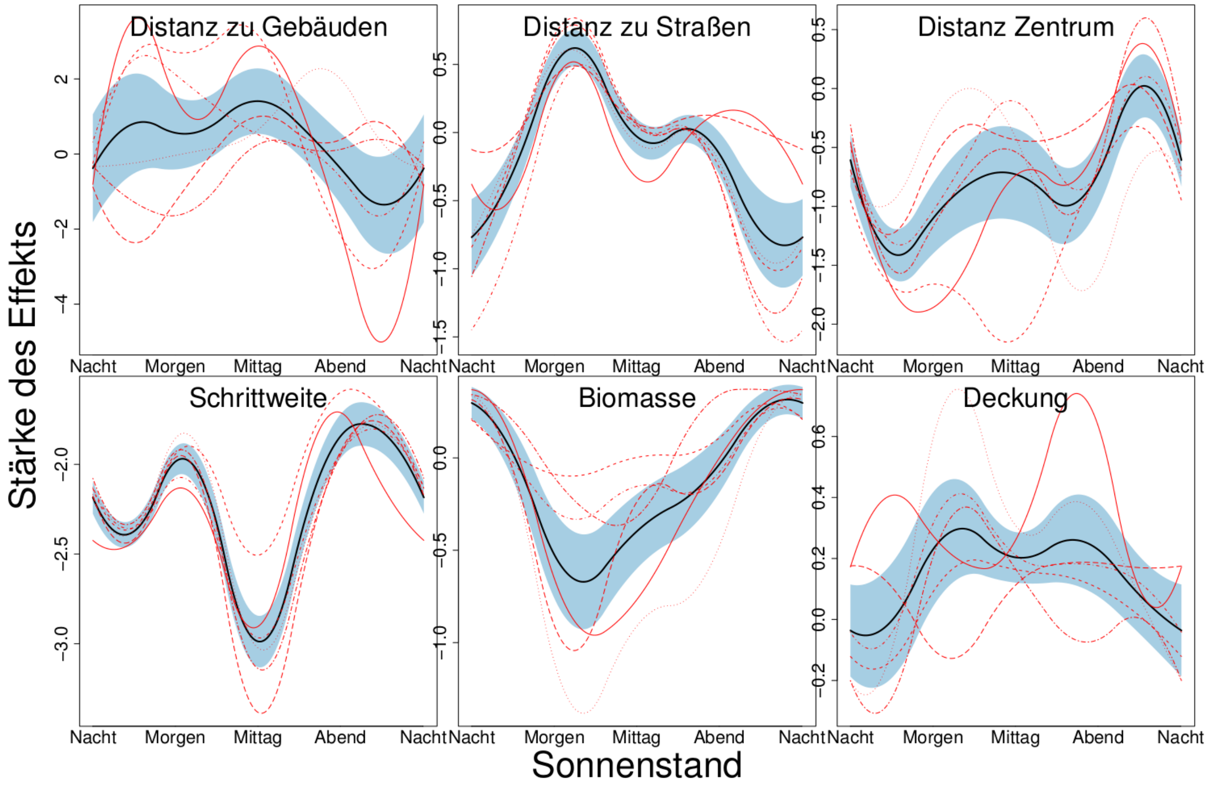

Abbildung 4: Stärke verschiedener Effekte auf die Bewegungsentscheidungvon Hirschen im Sommer im Tagesverlauf. Die schwarze Linie zeigt den Populationsmittelwert mit blauhinterlegtem Konfidenzintervall. Rote Linien: Schätzungen für einzelne Individuen, wobei jede Strichelung sich auf ein Individuum bezieht.

In Abb. 4 sind deutliche tageszeitliche Variationen in der Präferenz für alle Faktoren zu erkennen. Während für Biomasse stärker in der dunklen Tageshälfte selektiert wird (Abb. 4, unten Mitte), werden deckungsreichere Gebiete während des Tages aufgesucht (Abb. 4, unten rechts). Die Distanz (Schrittweite), die innerhalb einer

Stunde zurückgelegt wird, ist während der Dämmerung, insbesondere der Abenddämmerung, am höchsten und nimmt am Tag und in der Nacht ab. Diese Muster unterscheiden sich nicht signifikant zwischen Männchen und Weibchen (nicht gezeigt). Hingegen die Distanz zum Streifgebietszentrum (Abb. 4, oben rechts), die über den Tageslauf weitestgehend konstant ist, ist für die Männchen im Allgemeinen größer als die für die Weibchen, was auf ein größeres Streifgebiet schließen lässt. Die Männchen halten sich in einer größeren Entfernung zu Straßen auf als Weibchen, für Gebäude ist es entgegengesetzt. Des Weiteren sind für einzelne Faktoren, wie Deckung, Distanz zu Gebäuden und Streifgebietszentrum, markante individuelle Unterschiede erkennbar. Hingegen zeigen die Individuen für Schrittweite, Distanz zu Gebäuden und die Nutzung der Biomasse sehr einheitliche Muster.

Ein Mustervergleich zwischen realen Pfaden und simulierten Pfaden zeigt, dass das Modell in Bezug auf die ausgewählten Faktoren realistische Pfade nachsimulieren kann (nicht gezeigt). Auch visuelle Vergleiche von simulierten Pfaden mit denen aus GPS-Daten ermittelten Pfaden zeigen zufriedenstellende Ähnlichkeiten hinsichtlich Streckenverläufen und Clusterbildung (Abb. 5)

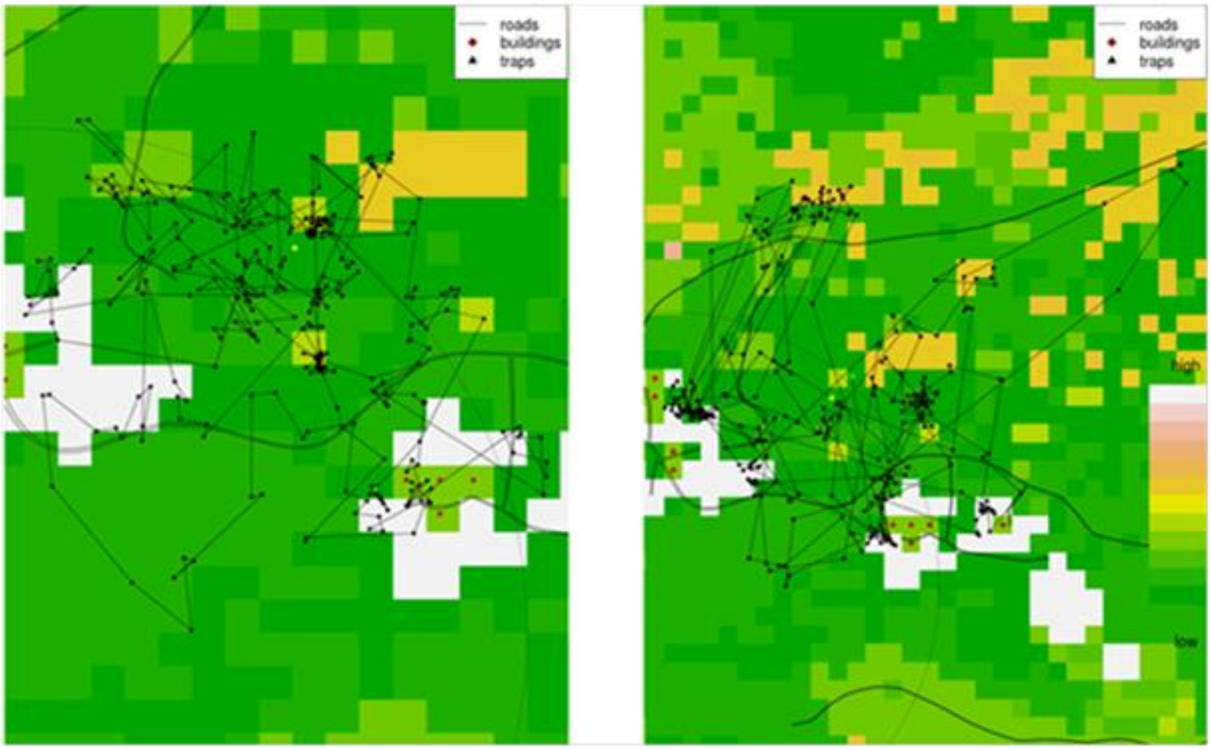

Abb. 5: Vergleich eines simulierten Pfads (links) mit dem eines adulten Weibchens (rechts). Die Karte zeigt die Biomasseverfügbarkeit, von dunkelgrün (wenig) bis weiß (viel).

4.6 Entwicklung von Szenarien für die Auswirkungen von Managementmaßnahmen auf die Raumnutzung von Rothirschen und Analyse der damit verbundenen räumlichen Muster der Verbissintensität

Ein Ziel des Projektes war die Entwicklung von Szenarien für die Auswirkungen von Managementmaßnahmen auf die Raumnutzung von Rothirschen und die Analyse der damit verbundenen räumlichen Muster der Verbissintensität. Als Managementmaßnahme war insbesondere die Auflösung der Wintergatter vorgesehen. Da die vollständige Auflösung der Gatter derzeit keine politisch realistische Maßnahme darstellt, wurden stattdessen Szenarien zu einem früheren Öffnungszeitpunkt untersucht.

Szenario 1: Frühere Öffnung der Gatter und Einstellung der Fütterung im Gatter
Szenario 2: Frühere Öffnung der Gatter und Weiterführung der Fütterung im Gatter
Szenario 3: Frühere Öffnung der Gatter und Einstellung der Fütterungen außerhalb des Nationalparks

Als Maß für die potentielle Verbiss- und Schälintensität, wurde die Aufenthaltsdauer von Rothirschen außerhalb des Nationalparks nach Öffnen der Wintergatter betrachtet. Die Auswirkungen veränderter Öffnungszeiten auf die Raumnutzung von Rothirschen wurden mittels einer individuen-basierten Modellierung untersucht. Einflussgrößen der Tierbewegung waren: (1) Distanz zur aktuellen Position, (2) Distanz zur Fütterungsstelle, (3) mittlere Kronenhöhe, und (4) absolute Distanz (in Tagen) zum stärksten Anstieg im NDVI. Der Zeitpunkt des stärksten Anstiegs im NDVI ist ein Maß für den Zeitpunkt der höchsten Futterqualität am entsprechenden Standort (Abb. 6). Die Parameter des Bewegungsmodells wurden mit mixed effects conditional logistic regression geschätzt. Dies erlaubt eine effiziente Schätzung der Parameter und die Berücksichtigung von Unterschieden zwischen Individuen. Zur Schätzung der Modellparameter wurden Daten von 18 weiblichen und 16 männlichen Rothirschen verwendet. Insgesamt lagen nach Ausdünnung auf zwei Stunden noch 62560 Positionen vor; pro Tier zwischen 193 und 5051 Positionen (Median: 1530).
Da keine genauen Angaben zur Verteilung von Fütterungen außerhalb des Nationalparks vorliegen, wurde ein Szenario mit hypothetischen Fütterungen entwickelt; 30 Fütterungen wurden entlang der Nationalparkgrenze in einem Abstand von 500 bis 1000 m mit einem Minimalabstand von 240 m zueinander zufällig verteilt.
Die mittlere Kronenhöhe wurde mittels LiDAR-Daten des Bayerischen Landesamtes für Digitalisierung, Breitband und Vermessung mit einer räumlichen Auflösung von 30 m bestimmt. Der Zeitpunkt des stärksten Anstiegs im NDVI wurde von MODIS-Daten für das Jahr 2010 aus 16-Tages-Kompositen bestimmt.

Die Simulation einer Trajektorie umfasste 504 Schritte mit einem Intervall von 2 Stunden; dies entspricht einem simulierten Zeitraum von 42 Tagen. Die Öffnungszeiten der Wintergatter wurden für einen Zeitraum vom 1. Februar bis zum bis 12. Mai in Zehntagesschritten variiert (11 Zeitpunkte). Die Sensitivität der Ergebnisse bezüglich von Schlüsselparametern wurde abgeschätzt, indem vier Szenarien betrachtet wurden, indem der Einfluss von Ergrünung einerseits und Distanz zu Fütterungen andererseits jeweils auf einen Standartwert und einen extremen Wert gesetzt wurden (Tabelle 1). Jede Kombination aus Öffnungszeitpunkt und Szenario wurde 25-fach wiederholt, d.h. insgesamt wurden 11 x 4 x 25 = 1100 Trajektorien von je 504 Schritten simuliert.

Alle Analysen wurden mit R Version 3.0.2 durchgeführt; die mixed effects conditional logistic regression wurde mit dem Paket TwoStepCLogit in Version 1.2.2 durchgeführt.

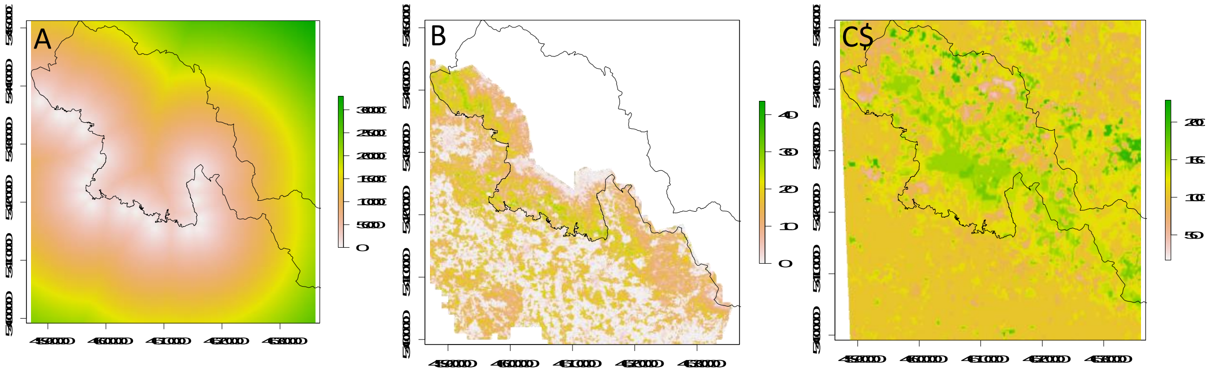

Abbildung 6: Karten der erklärenden Variablen des Rothirsch-Bewegungsmodells für die Managementszenarien: a) Distanz zu Fütterungen (m), b) Mittlere Kronenhöhe (m), c) Tag des stärksten Anstiegs im NDVI ("day of maximum greening") (Tag des Jahres). Projektion: DHDN.

Drei der vier betrachteten Einflussfaktoren auf das Bewegungsverhalten sind statistisch signifikant; lediglich der Zeitpunkt maximaler Ergrünung zeigt keinen statistisch signifikanten Effekt (Tabelle 1).

Tabelle 1: Modellparameter für das Bewegungsmodell. Dargestellt sind die Standardparameter (d.h. Schätzwerte für die *mixed effects conditional logistic regression*). Für die Szenarien zum Einfluss erhöhter Werte von Ergrünung und Distanz zur Fütterung wurden folgende Werte verwendet: Erhöhte Werte für Ergrünung: -0.041; Distanz zur Fütterung: -0.003. Als Maß für die Variation zwischen Individuen kann die Standardabweichung des *random effects* herangezogen werden: Distanz: 0.0013, Ergrünung: 0.016, Kronenhöhe: 0.033, Fütterung: 0.0009.

Variable	Koeffizient	SE	Z
Distanz	-0.0027	0.0002	-11.88
Absolute Differenz zum Zeitpunkt maximaler Ergrünung	-0.0004	0.0031	-0.13
Mittlere Kronenhöhe	-0.0633	0.0060	-10.52
Distanz zu Fütterung	-0.0008	0.0002	-4.79

Die simulierten Bewegungsmuster variieren beträchtlich zwischen verschiedenen Wiederholungen (Abb. 7). Der Anteil von Positionen außerhalb des Parks variierte in einem Fall von 0% bis über 90% für dieselben Randbedingungen. Insbesondere in den Szenarien mit erhöhter Attraktivität von Fütterungen war die Variabilität jedoch erheblich reduziert.

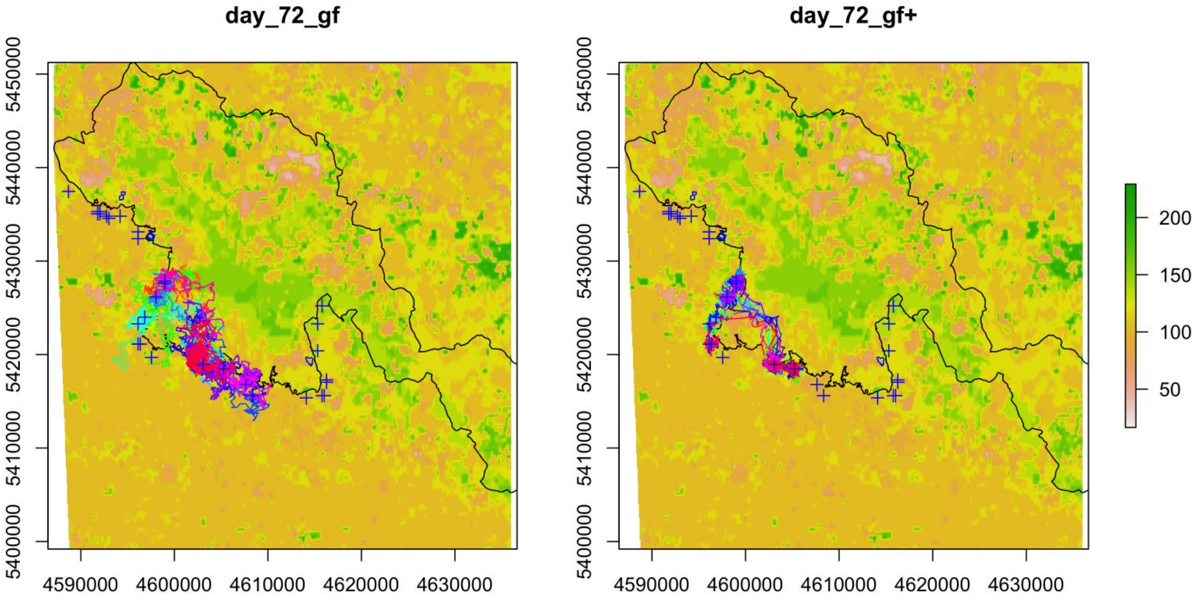

Abbildung 7: Simulierte Bewegungstrajektorien von Rothirschen. A) Standardszenario; B) Erhöhter Effekt der Distanz zu Fütterungen. Der simulierte Zeitraum umfasst 42 Tage, die zeitliche Auflösung beträgt zwei Stunden. Jeweils 25 Wiederholungen sind dargestellt. Blaue Kreuze bezeichnen die (hypothetischen) Fütterungen. Ausgangspunkt ist jeweils das Wintergatter Neuhüttenwiese.

Im Wesentlichen zeigen zwei Ergebnisse mit Praxisrelevanz. Erstens hat der Zeitpunkt der Öffnung der Wintergatter in den Simulationen keinen klaren Effekt auf den Anteil der simulierten Positionen außerhalb des Nationalparks während der ersten 42 Tage nach Öffnung der Wintergatter. Zweitens ist der in den Simulationen wesentliche Einflußfaktor für den Anteil der Positionen von Rothirschen außerhalb des Nationalparks die Attraktivität der Fütterungen.

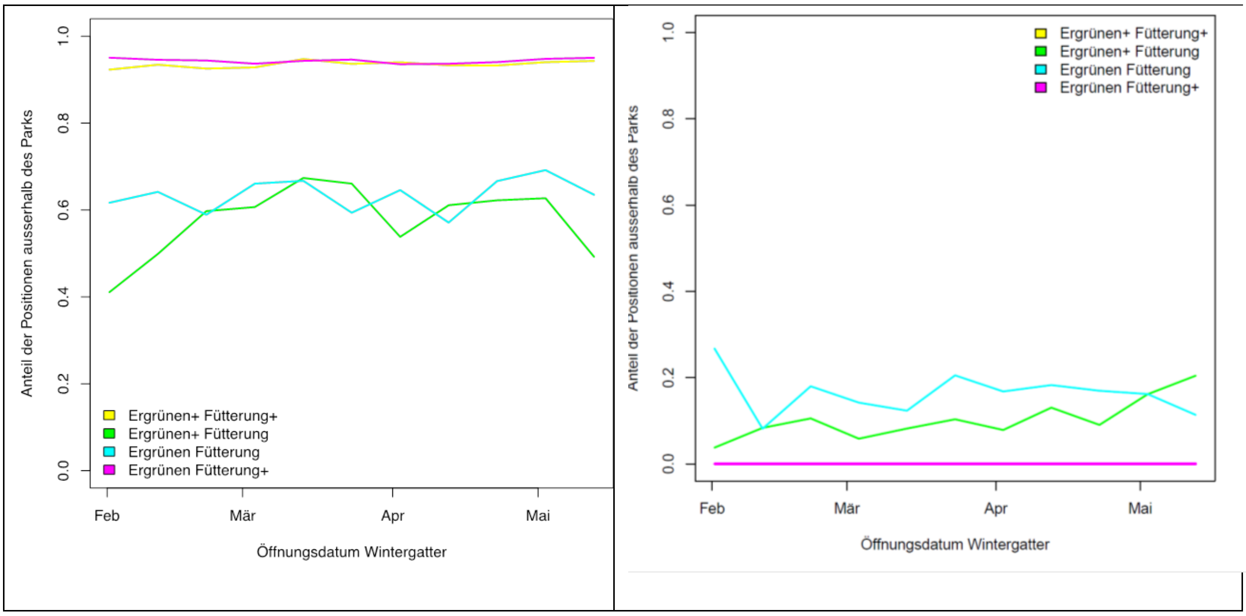

Abbildung 8: Simulierter Anteil der Positionen außerhalb des Nationalparks innerhalb von 42 Tagen nach Öffnen der Wintergatter. Dargestellt ist der Mittelwert von 25 Wiederholungen. Rechts: Ohne Fütterung im Wintergatter. Links: Mit Fütterung im Wintergatter. In der Legende ist jeweils dargestellt, ob das Ergrünen der Vegetation berücksichtigt und in den Gebieten außerhalb des Nationalparks gefüttert wurde (+) oder nicht ().

Zweitens ist die Fortführung der Fütterung in den Wintergattern ein wichtiger Faktor zur Schadensreduktion. Ohne Fütterung in den Gattern und bei Fütterung außerhalb des Nationalparks wandern die meisten Tiere zu den Fütterungen. Selbst wenn die Fütterungen außerhalb des Nationalparks nicht betrieben werden muss damit gerechnet werden, dass viele Tiere das Nationalparkgebiet verlassen. Wird jedoch die Fütterung in den Wintergattern weiter betrieben, bleiben in jeder Variante mehr als 80 % der Tiere im Nationalparkgebiet (Abb. 8).

Die vorliegenden Ergebnisse zeigen, dass es möglich ist, aufgrund von Telemetriedaten zum Bewegungsverhalten von Individuen und Fernerkundungsinformationen zur Beschreibung von Umweltbedingungen statistische individuen-basierte Bewegungsmodelle zu konstruieren und deren

Parameter zu schätzen. Diese Modelle können verwendet werden, um mögliche Auswirkungen von Managementalternativen auf die Raumnutzung abzuschätzen. Im vorliegenden Fall ist eine wesentliche Einschränkung für die Belastbarkeit der Modelle, dass sich das Bewegungsverhalten von Rothirschen im Jahresverlauf verändert. Die jetzt vorliegende methodische Infrastruktur stellt eine hervorragende Grundlage dar, um experimentelle Variationen der Öffnungszeiten der Gatter zu begleiten und ähnlich gelagerte Managementfragen zu untersuchen.

Auf Basis der oben vorgestellten Simulationsergebnisse des Modellansatzes wurde von der Nationalparkverwaltung im Winter 2012/2013 ein Experiment durchgeführt, um die Auswirkungen einer früheren Wintergatteröffnung in der Praxis zu testen. Dazu wurden in jedem der vier Wintergatter 5 adulte Weibchen mit Halsbandsendern ausgestattet und zwei Gatter früher geöffnet. Anschließend wurden die Bewegungsmuster in einem einstündigen Turnus aufgezeichnet und die Schäle der besenderten Tiere im Gelände erfasst.

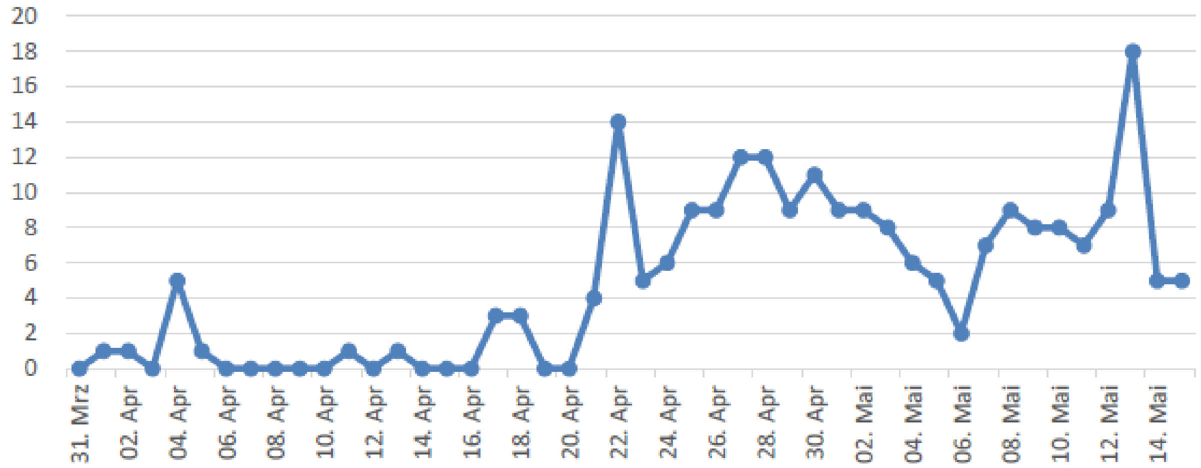

Abb. 9: Verlauf der Entwicklung der Schäle nach Öffnung der Wintergatter Ahornschachten und Neuhüttenwiese am 31.3.2013.

Obwohl die Wintergatter Ahornschachten und Neuhüttenwiese bereits Ende März geöffnet wurden, verließen die Tiere die Gatter zunächst nur für kurze Ausflüge. Deshalb konnten in den ersten Woche nach Öffnung der Gatter auch fast keine Schäle beobachtet werden. Der Verlauf der Schälhäufigkeit zeigt deutlich, das in der Periode vor der regulären Öffnung der Gatter weniger Schäle gefunden wurde als nach der regulären Öffnung (Abb. 10). Die neun in den beiden Wintergattern beobachteten Tiere hielten sich sowohl im April, als auch im restlichen Jahr nur in den Nationalparken Sumava und Bayerischer Wald auf. Einzige Ausnahme bildete ein Weibchen vom Wintergatter Ahornschachten, das den Nationalpark für einen halben Tag verließ (Abb. 9).

Aus den Ergebnisse der Simulation und des Experiments kann die Schlussfolgerung gezogen werden, dass eine frühere Öffnung der Wintergatter weder zu einer Abwanderung der Rothirsche ins Umfeld des Nationalparks, noch zu einer erhöhten Schälhäufigkeit führt. Voraussetzung ist allerdings, dass die Fütterung innerhalb der Gatter nicht gestoppt wird.

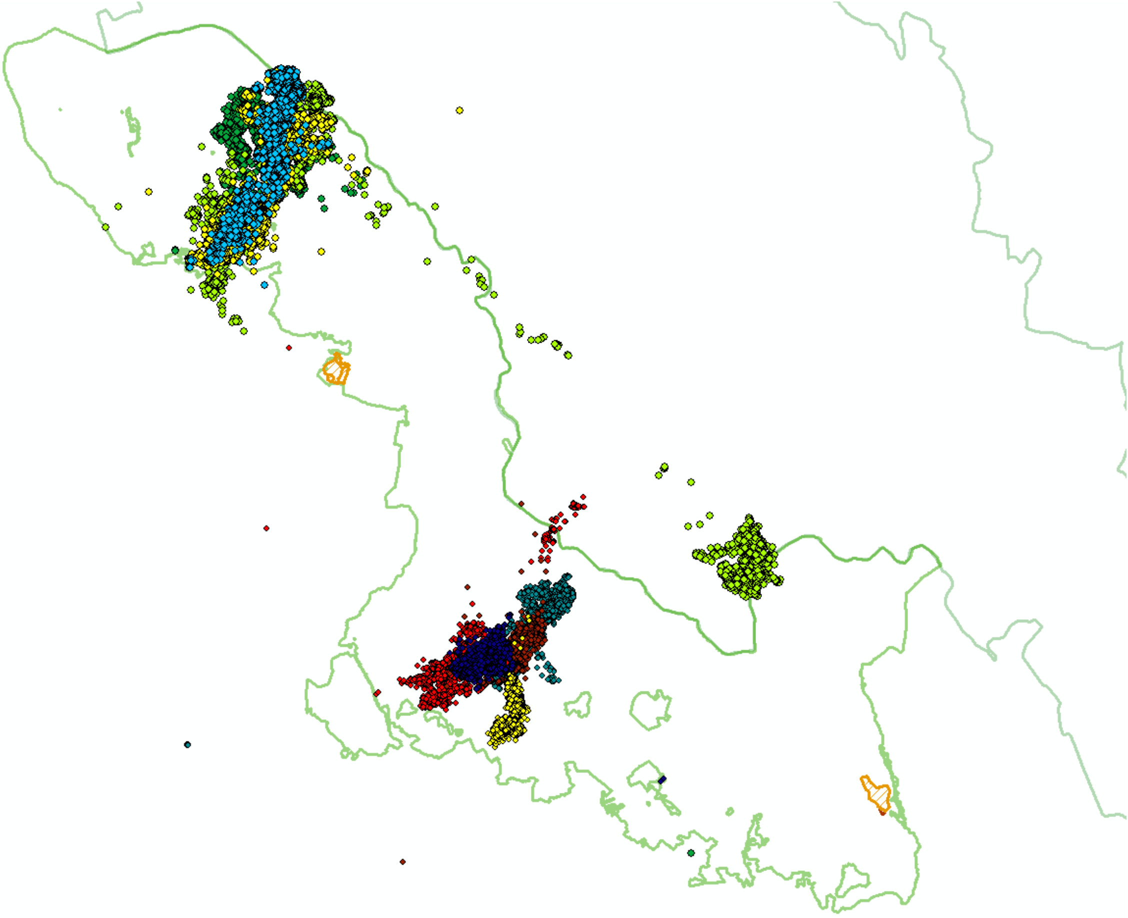

Abbildung 10 : Positionen von 9 adulten Weibchen, die in den Wintergattern Ahornschachten und Neuhüttenwiese besendert wurden. Obwohl die Wintergatter bereits am 31.3 geöffnet wurden machte nur ein Weibchen aus dem Wintergatter Ahornschachten einen kurzen Ausflug von einem halben Tag aus dem Nationalparkgebiet.

Die in diesem Projekt entwickelten Modelle zur Analyse der Streifgebiete und der Analyse der Habitatnutzung innerhalb der Streifgebiete befinden sich als Zipfile in Anlage 10 zu diesem Bericht:

c) Individuen-basierte Modelle.zip

5 Modell der Interaktion von Pflanzenfressern und der Walddynamik (Wald-Wild)

Durch forstwirtschaftliche Eingriffe wurden die Waldstrukturen in Mitteleuropa in den vergangenen Jahrhunderten stark verändert. Auch auf dem Gebiet des Nationalparks Bayerischer Wald wurden die Waldflächen seit Mitte des 19. Jahrhunderts fortwirtschaftlich genutzt, was zu starken Veränderungen im Aufbau und der Baumartenzusammensetzung führte. Besonders hervorzuheben sind hierbei der Rückgang der Tanne, deren Anteil von 30% zu Beginn der geregelten Forstwirtschaft auf heute unter 3% zurückging und die Umwandlung von naturnahen Bergmischwäldern, deren Fläche um 1900 in den Staatswäldern des Bayerischen Waldes noch 14.000 ha betrug, hin zu strukturarmen Altersklassenwäldern. Ein Ziel des Wildtiermanagements im Nationalpark Bayerischer Wald ist es deshalb, den Verbiss auf ein Niveau zu senken, dass die Etablierung der Tanne ermöglicht, so dass deren Anteil wieder ansteigen kann. Erschwert wird diese Aufgabenstellung durch die globale Klimaveränderung, die zu einer Veränderung der Walddynamik mit Auswirkungen auf die Verjüngung, das Wachstum und die Mortalität von Baumindividuen führt. Deshalb sollte in diesem Teilprojekt die Auswirkung verschiedener Verbissintensitäten und –dynamiken unter Berücksichtigung verschiedener Klimaszenarien auf die Waldentwicklung im Nationalpark untersucht werden.

Dafür wurde im ersten Schritt die Verbissvariabilität im Nationalparkgebiet für die verschiedenen Baumarten untersucht. Auf dieser Basis wurden neue Gleichungen im Waldmodell FORCLIM V.3 implementiert und anschließend die Entwicklung typischer Waldbestandestypen des Nationalparkgebietes unter verschiedenen Verbiss- und Klimaszenarien simuliert.

Die Modelle sagen einen starken Rückgang der Fichten und Tannen aufgrund vermehrter Trockenperioden im Sommer und milder Wintertemperaturen voraus. Die Folgen der Klimaveränderungen haben mittelfristig (~100 Jahre) einen positiven Einfluss auf die Baumartenvielfalt, während langfristig (1000 Jahre) sowohl die Baumartenvielfalt als auch die Bestandesgrundfläche gegenüber den Modellläufen mit dem aktuellen Klima zurückgehen. Auf der anderen Seite hat der Verbissdruck unter dem aktuellen Klima durch selektiven Verbiss und Veränderungen des Lichtregimes einen starken Einfluss auf die Baumartenzusammensetzung, während die Waldentwicklung unter den Klimaveränderungszenarien nicht signifikant durch den Verbissdruck verändert wird. Für stark verbissgefährdete Arten kann selbst Nullverbiss den Rückgang der trockenheitssensitiven Arten nicht aufhalten.

Damit kann die Limitation von Huftierbeständen ein wichtiges Instrument zur Erhöhung der Diversität von fichtendominierten Wäldern sein. Allerdings gilt das nur für die aktuellen klimatischen Bedingungen. Unter den prognostizierten Klimaveränderungen hat der Verbiss nur einen geringen Effekt auf die Entwicklung der Baumartenzusammensetzung.

Die detaillierten Ergebnisse dieser Studie finden sich in der Anlage zu diesem Bericht (Anlage 4):

Cailleret M., Heurich, M. and H. Bugmann. Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. Submitted to Forest Ecology and Management.

Das in diesem Projekt verbesserte Modellierungssoftware FORCLIM V.3 kann von der Professur für Waldökologie der ETH-Zürich für interessierte Anwender zur Verfügung gestellt werden. Weitere Informationen finden sich unter: http://www.fe.ethz.ch/research/standdynamics/forclim_model/index_EN

6 Diskussion der Zielerreichung des Projektes

Gegenüber dem im Projektantrag geplanten Projektablauf kam es aus zwei Gründen zu einer erheblichen zeitlichen Verzögerung. Erstens war es zu Begin des Projektes nicht möglich die ausgeschriebene Stelle einer Modelliererin rechtzeitig mit einer geeigneten Person zu besetzen. Dadurch verschob sich der Projektanfang auf September 2009. Zweitens ergaben sich Finanzierungsprobleme beim Schweizer Projektpartner Eidgenössisch Technische Hochschule Zürich. Durch die Aufwertung des Schweizer Frankens gegenüber dem Euro war es zunächst nicht möglich, die geplante Post-Doc-Stelle für einen ausreichend langen Zeitraum zu finanzieren. Erst durch Umschichtungen innerhalb der ETH gelang es einen Mitarbeiter für einen ausreichend langen Zeitraum zur Bearbeitung der Fragestellung einzusetzen. Dadurch ergab sich eine weitere Verzögerung von 9 Monaten.

Im Rahmen der Projektbearbeitung kam es zu zwei Änderungen und drei Erweiterungen gegenüber der ursprünglich geplanten Vorgehensweise. Aufgrund der Ablehnung der Initiative „Rothirsch auf neuen Wegen“, deren Ziel die Entwicklung eines großflächigen Rothirschmanagements mit Aufgabe der Wintergatter und Erweiterung des Rotwildgebietes war, durch die Vereinigungen der Waldbesitzer und Jäger im Vorfeld des Nationalparks, war es nicht mehr möglich, einvernehmliche Szenarien für die Auflösung der Wintergatter mit den Interessengruppen zu entwickeln. Deshalb wurden Szenarien entwickelt, die auch eine Chance auf Realisierung haben, nämlich Szenarien zur früheren Öffnung der Gatter. Der alleinige Modellansatz wurde um einen experimentellen Ansatz erweitert, um die Auswirkungen einer früheren Gatteröffnung in der Realität zu überprüfen. Dazu wurden in den 4 Gattern jeweils 5 Tiere besendert und zwei Gatter 1 Monat früher geöffnet. Auch war es entgegen dem geplanten Vorgehen nicht möglich die Bewegungsmuster der Huftiere mit dem Verbiss zu koppeln, da sich aus den Telemetriedaten (Positions- und Aktiviätsdaten) die Verhaltensweise Fressen nicht klassifizieren ließ. Zur Kopplung der Tiere mit dem Waldmodell griffen wir deshalb auf die Verbissdaten der Waldinventur der Nationalparkverwaltung zurück. Diese haben den Vorteil, dass Verbiss- und Waldstrukturdaten, die anschließend für die Simulationen verwendet werden, am gleichen Ort erhoben werden. Bei den Simulationen zum Einfluss des Verbisses auf die Waldentwicklung wurde der ursprüngliche Ansatz des Projektes erweitert und zusätzlich Simulationen unter der Annahme von Klimaprognosen durchgeführt. Dadurch kann nicht nur gezeigt werden, welchen Einfluss der Verbiss unter den aktuellen klimatischen Verhältnissen hat sondern auch, wie sich die Managementmaßnahmen unter den veränderten Bedingungen der Klimaveränderungen auswirken. Erweitert wurde der ursprüngliche Projektansatz auch durch die Analyse von Daten aus den Beschleunigngssensoren der Halsbänder, aus deren Analyse Hinweise zu einer Verbsserung des Wildtiermanagementes abgeleitet werden können.

7 Öffentlichkeitsarbeit

Insgesamt konnte das Projekt mit 30 Vorträgen und Führungen der Öffentlichkeit vorgestellt werden. Darunter fanden sich Vorträge für die allgemeine Öffentlichkeit, genauso wie für spezielle Zielgruppen, wie die Hochwildhegegeinschaft Bayerischer Wald. Darüber hinaus wurden Projektergebnisse auch auf wissenschaftlichen Tagungen z.B. der Jahrestagung der Gesellschaft für Ökologie oder der Tagung der European Roe Deer Group vorgestellt. Bei den Präsentationen wurde jeweils auf die Projektförderung durch die Deutsche Bundesstiftung Umwelt hingewiesen und das Logo präsentiert. Eine Liste aller Vorträge findet sich in der Anlage zu diesem Bericht.

Die Ergebnisse des Projektes wurden auch auf einer Fachtagung der Nationalparkverwaltung dem deutschsprachigen Fachpublikum vorgestellt. Im Tagungsflyer wurde auf die Förderung durch die Deutsche Bundesstiftung Umwelt aufmerksam gemacht. Der Tagungsflyer befindet sich in der Anlage zu diesem Bericht. Darüber wird auch auf der Homepage der Wildtierforschung der Nationalparkverwaltung Bayerischer Wald www.luchserleben.de auf die Förderung durch die DBU hingewiesen.

Im Rahmen des Projektes wurden bislang sechs wissenschaftliche Manuskripte erstellt, deren Inhalt in diesem Bericht wiedergegeben wird und die sich in der Anlage befinden. Die Manuskripte wurden bereits bei internationalen wissenschaftlichen Zeitschriften eingereicht oder sollen in naher Zukunft eingereicht werden. Zwei Manuskripte befinden sich in der Überarbeitung und sollen in Kürze eingereicht werden. In den Manuskripten wird jeweils auf die Förderung durch die Deutsche Bundesstiftung Umwelt hingewiesen. Bei Annahme eines Manuskriptes zur Publikation, wird diese Arbeit der Deutschen Bundesstiftung Umwelt jeweils als PDF-Datei umgehend zur Verfügung gestellt. In Zukunft sind noch weitere Publikationen aus dem Projekt zu erwarten, diese werden nach Publikation ebenfalls der Deutschen Bundesstiftung Umwelt zur Verfügung gestellt.

Um einen Transfer der Ergebnisse in die Diskussion um das Wildtiermanagement in Deutschen Nationalparken zu gewährleisten, wurden die Projektergebnisse den Mitarbeitern des Projektes „Wildtiermanagement in deutschen Nationalparken“ vorgestellt. Im Rahmen dieses Projektes sollen Kriterien für eine Evaluierung des Wildtiermanagements in allen deutschen Nationalparken erarbeitet werden. Die in dem Projekt „Modelluntersuchungen zum Wildtiermanagement“ vorgestellten

Ergebnisse und Grundlagen können somit direkt in die Arbeiten zum Wildtiermanagement in deutschen Nationalparken einfließen. Auch die entwickelten Modelle stehen anderen Nutzern zur Verfügung und befinden sich in Anlage zu diesem Bericht. Die Mitarbeiter der Nationalparkverwaltung Bayerischer Wald wurden im Umgang mit diesen Modellen geschult, so dass die Projektergebnisse auch in Zukunft verwendet werden können.

8 Fazit und Ausblick

Die Ergebnisse der Forschungsarbeiten dieses Projektes zeigen, dass im Laufe der über 40 Jährigen Nationalparkgeschichte nach starken jagdlichen Eingriffen in den ersten 15 Jahren die Intensität des Wildtiermanagements Schritt für Schritt zurückgeführt werden konnte. Dabei hat sich auch die Zielstellung des Handelns von einer rein forstlichen Orientierung hin zu einer ökologischen, prozesschutzorientierten Sichtweise verändert.

Die Analysen zur Verteilung des Verbissdrucks zeigen aber immer noch einen starken Einfluss des Managements auf die Waldökosysteme des Nationalparkgebietes, die der Nationalparkzielsetzung einer möglichst wenig vom Menschen gesteuerten Entwicklung entgegenlaufen. Eine weitere Rückführung der Eingriffe durch die Nationalparkverwaltung ist deshalb wünschenswert im Sinne der Nationalparkidee. Die Analyse der Habitatnutzung innerhalb der Streifgebiete macht deutlich, dass das Ziel Wildtiere erlebbar zu machen im Nationalparkgebiet nicht erreicht ist. Rehe und Rothirsche meiden bei Tag die Nähe zu Menschen und suchen, ähnlich wie in bejagten Gebieten, tagsüber Dickungskomplexe auf, um sich zu verbergen und das trotz einer unbejagten Fläche von 17000 ha. Dadurch stellt sich die Frage, ob das Ziel einer Erlebbarkeit von Wildtieren, wie man sie aus den Nordamerikanischen Parken kennt, in Mitteleuropäischen Waldnationalparken überhaupt erreichbar ist. Zum einen sind die Schutzgebiete relativ klein, so dass in den Streifgebieten der Tiere immer auch Bereiche mit Jagdausübung umfassen, zum anderen führen die dichten Wälder dazu, dass die Tierdichten gering sind und die Tiere schlecht beobachtet werden können. Diese Frage kann mit den vorliegenden Daten nicht geklärt werden. Hierzu sind Analysen notwendig, die die Daten verschiedener Schutzgebiete miteinander vergleichen. Die aktuell durchgeführten Maßnahmen zur Bestandeskontrolle scheinen deshalb weiterhin das Verhalten der Tiere zu beeinflussen und sollten räumlich und zeitlich weiter eingeschränkt werden. Die Analysen zum Aktivitätsverlauf der Rothirsche machen deutlich, dass die Tiere bereits ab Anfang April ihre Aktivität erhöhen und einen größeren Bewegungsdrang

haben. Die Simulationen und das Experiment zur früheren Öffnung der Wintergatter verdeutlichen, dass diese Maßnahme nicht wie befürchtet zu einem starken Anstieg der Schäle führt und Wälder außerhalb des Nationalparks nicht betroffen sind.
Schließlich zeigen die Simulationen verschiedener Szenarien zur Waldentwicklung in den nächsten 100 und 1000 Jahren, dass jagdliche Maßnahmen zur Reduktion des Verbisses (selbst bei Ausschluss jeglichen Verbisses) im Vergleich zu den Veränderungen, die durch den globalen Klimawandel prognostiziert werden nur eine geringe Wirkung zeigen. Sollten sich die Prognosen bestätigen wird dadurch die Sinnhaftigkeit von Wiltierkontrolle in Schutzgebieten in Frage gestellt.

Auf Basis dieser Forschungsergebnisse und unter Einbeziehung der Ergebnisse des Luchsprojektes der Nationalparkverwaltung, das 2013 abgeschlossen wurde, können Vorschläge unterbreitet werden, um die Intensität des Wildtiermanagements auf dem Gebiet des Nationalparks weiter zu reduzieren, um dem Ziel einer weitgehend vom Menschen unbeeinflussten Entwicklung näher zu kommen.

Der Schwerpunkt bei den folgenden Empfehlungen liegt auf Veränderungen, die von der Nationalparkverwaltung autonom umgesetzt werden können. Ein großer Schritt zur Verringerung der Managementintensität konnte im Projektzeitraum bereits bei der Regulierung der Rehbestände gemacht werden. Hier wurden alle Maßnahmen zur Bestandeskontrolle, sowie die bis dahin getätigten Forschungsabschüsse für die Umweltprobenbank im gesamten Nationalparkgebiet im Jahr 2012 eingestellt. Damit unterliegt die Rehpopulation auf Nationalparkgebiet weitestgehend natürlichen Faktoren. Beispielsweise ist der Hauptmortalitätsfaktor für die besenderten Rehe die Prädation durch den Luchs, gefolgt von Abschüssen außerhalb des Nationalparks. Auch die natürlichen Wanderbewegungen zwischen dem Nationalpark und dessen Vorfeld sind durch Auflösung von Fütterung und Kirrung wieder in Gang gekommen.

Beim Rothirsch ist die Intensität des Wildtiermanagements ungleich höher als beim Reh, insbesondere durch die Wintergatter, in denen sich die Tiere von Ende Oktober bis Ende April, also maximal 6 Monate, aufhalten. Aktuell beträgt die Zone ohne Rothirschmanagement 17160 ha, das entspricht knapp 71% der Nationalparkfläche. Wir empfehlen für das Rothirschmanagement, dass die Vorgaben der IUCN für Schutzgebiete der Kategorie II umgesetzt und 75% der Fläche frei von Wildtiermanagement gestellt werden. Um dieses Ziel zu erreichen, müsste die Fläche ohne Wildtiermanagement nur um 1030 ha vergrößert werden. Damit könnte der Nationalpark Bayerischer Wald als erster Deutscher Nationalpark die 75%-Regel beim Wildtiermanagement erfüllen und dadurch eine Vorreiterrolle einnehmen. Zur Umsetzung wird vorgeschlagen, die Rothirschregulierung im Rachel-Lusen-Gebiet

außerhalb der Gatter vollständig einzustellen. Um zu vermeiden, dass Rothirsche und Rehe in ihrem natürlichen Bewegungsverhalten beeinflusst werden und ggf. lokal erhöhte Wildtierdichten auftreten, sollte die Kirrung im gesamten Nationalparkgebiet außerhalb der Saufänge und Wintergatter eingestellt werden.
Für das Wintergattermanagement ergeben sich aus den Forschungsergebnissen die folgenden Empfehlungen: Um den erhöhten Verbiss im Umfeld der Gatter zu reduzieren, sollten die Lockfütterungen zum Fangen von Rothirschen in den Vorfanggattern nach dem Ende der Jagdzeit eingestellt werden. Dadurch kann vermieden werden, dass sich die Tiere im Umfeld der Gatter konzentrieren und es dort zu einem erhöhten Verbiss kommt. Darüber hinaus kann aus den Ergebnissen der Analyse der Aktivitätsdaten, sowie der Simulationen und dem Rothirschexperiment geschlossen werden, dass die Wintergatter früher geöffnet werden sollen, um den Zeitraum, den sich die Tiere im Gatter aufhalten möglichst gering zu halten und dem Verhalten der Tiere anzupassen.

Weitere Schritte hin zu einer Verbesserung des Wildtiermanagements, die über die Parkgrenzen hinaus gehen, wie der Veränderung der Abgrenzung des Rotwildgebietes und der Auflösung der Wintergatter sind nach der Ablehnung des Projektes „Rothirsch auf neuen Wegen“ auf absehbare Zeit nicht umsetzbar.

Schlüsselelement für das Gelingen sämtlicher über die Schutzgebietsgrenzen hinausreichenden Verbesserungen im Umgang mit Wildtieren ist eine ausreichende Akzeptanz bei den betroffenen Interessensgruppen. Im Sinne eines „ecosystem approach“ muss die lokale Bevölkerung informiert und in entsprechende Projekte eingebunden werden. Dafür ist ein es notwendig in zwei Bereichen zu arbeiten:

Erstens Fortführung der auf Wildtiere bezogenen Bildungs- und Öffentlichkeitsarbeit um Interesse und Verständnis zu generieren. Dabei sollte insbesondere auch für die Akzeptanz großer Beutegreifer geworben werden, deren Rückkehr in den nächsten Jahren das zentrale Thema im Wildtiermanagement sein wird.
Zweitens regelmäßiger, im günstigsten Falle auch institutionalisierter Austausch mit Jägern, Förstern, Waldbesitzern und Landwirten im Vorfeld des Nationalparks und einer Zusammenarbeit mit diesen Gruppen in konkreten Projekten.

Die aus der Analyse der Geschichte des Umgangs mit Wildtieren und den Forschungsergebnissen gezogenen Erkenntnisse für das Wildtiermanagement des Nationalparks können auch auf andere Mittelgebirgsnationalparks Mitteleuropas mit ausgeprägter Saisonalität zwischen Winter- und Sommerhalbjahr übertragen werden:

1. Ein Zeitraum von 20 Jahren reicht aus, die Huftierbestände auf eine Dichte zu senken, die eine Verjüngung der Hauptbaumarten ermöglicht. Anschließend kann die Intensität des Managements zurückgeführt werden, so dass nach dem Übergangszeitraum von 30 Jahren das Ziel, auf 75% der Nationalparkfläche kein Wildtiermanagement zu nicht mehr einzugreifen, erreicht werden kann.

2. Fütterungen und Kirrungen sollen auf dem gesamten Nationalparkgebiet nicht eingesetzt werden.

3. Die Wildtierkontrolle soll zeitlich und räumlich stark beschränkt stattfinden. Der Einsatz von effektiven Methoden, wie beispielsweise Saufängen und Gatterabschüssen ist dafür notwendig.

4. Die Rückkehr von großen Beutegreifern wie Luchs und Wolf ist eine wichtige Voraussetzung für die Entwicklung einer natürlichen Dynamik und sollte von den Nationalparkverwaltungen aktiv durch Bildungs- und Akzeptanzarbeit unterstützt werden.

9 Anlagen

Anlage 1:

Heurich M. und K. Engelhardt: Entwicklung des Huftiermanagements im Nationalpark Bayerischer Wald. Der lange Weg zum nationalparkgerechten Umgang mit Huftieren.

Anlage 2:

Möst, L., Hothorn T., Müller, J. and Heurich M.: How to manage ungulates in a national park? Unintended side effects of management measures on the distribution of browsing pressure in the landscape. Submitted to Journal of Environmental Management.

Anlage 3:

Bevanda, B., Fronhofer, E.A., Heurich, M. and Reineking B. What determines home range size? The importance of a landscape's spatial configuration.

Anlage 4:

Dupke, C., Reineking, B., Ewald, M.,, Zeppenfeld, T., Heurich, M.: Resource distribution explains temporal dynamics in habitat use by European roe deer.

Anlage 5:

Ewald, M., Claudia Dupke, C., Heurich, M., Müller, J. and Reineking, B.: The application of LiDAR remote sensing and activity sensors to analyze winter habitat selection of European roe deer.

Anlage 6:

Berger, A., Krop-Benesch, A., Hofer H. and M. Heurich: Seasonal variation in circadian activity patterns in red deer (Cervus elaphus) in Bavarian Forest National Park

Anlage 7:

Cailleret M., Heurich, M. and H. Bugmann. Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. Submitted to Forest Ecology and Management.

Anlage 8:

Liste der Vorträge und Führungen

Anlage 9:

Flyer Fachtagung Nationalparkverwaltung

Anlage 10 :

a Modelle zur Analyse der Streifgebiete

b Modelle zur Analyse der Habitatnutzung

c Individuen-basierte Modellierung

Anlage 1:

Entwicklung des Huftiermanagements im Nationalpark Bayerischer Wald

Der lange Weg zum nationalparkgerechten Umgang mit Huftieren

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Ziel dieses Artikels ist es, die Entwicklung des Huftiermanagements im Verlauf von 40 Jahren Nationalparkgeschichte zu rekonstruieren. Es soll die Frage beantwortetet werden, welche Leitbilder, Grundsätze und Motivationen es für das Schalenwildmanagement gab und wie diese auf der Fläche umgesetzt wurden. Zur Rekonstruktion der Geschichte des Huftiermanagements wurden drei Methoden eingesetzt - eine Literaturstudie, Interviews von aktuellen und ehemaligen Nationalparkmitarbeitern und die Analyse der Abschussmeldungen.

Jagd- und Hegepraxis vor der Nationalparkgründung

Die Bestände von Rot- und Rehwild waren Ende der 1960er Jahre im Inneren Bayerischen Wald sehr hoch. Zudem wurde von 1953 bis 1970 das jährliche Abschusssoll durchschnittlich nur zu etwa 70% erfüllt (Wotschikowsky 1981, S. 24).

Eine Kette von Winterfütterungen sollte v.a. die jagdlich begehrten Rothirsche am saisonalen Wandern in tiefer gelegene Lagen hindern (StMELF (Hrsg.) 1975, S.17). Es gab ca. 43 Schalenwildfütterungen über das heutige Altgebiet verteilt, davon 20 „reine“ Rehwildfütterungen und 23 Rotwildfütterungen, die jedoch von beiden Wildarten aufgesucht wurden (Hack 1988, S.6); auch Wotschikowsky (1981) geht von ursprünglich über 40 Winterfütterungen aus. Damalige Revierleiter berichten von der Problematik, dass mit dem zur Verfügung stehende Futter der Nahrungsbearf der hohen Wildbestände nicht gedeckt werden konnte. Der Futteretat für die Forstämter des Bayerischen Waldes war weitaus geringer als der der Hochgebirgsforstämter. Meist stand also nicht genug Heu für den ganzen Winter zur Verfügung. „Die Fütterung war damals wie eine schlechte Kirrung – man hat die Hirsche da hingelockt und sie dann vor leeren Trögen stehen lassen“ (J4). Die Folge dieser

Wildkonzentrationen waren schwerwiegende Schäl- und Verbissschäden, besonders rund um die Fütterungen.

Aus einer von der Forsteinrichtung im Jahr 1972 erstellten Schälschadenskarte (Karte. 1) lassen sich die Standorte dieser Fütterungen, sowie das Ausmaß der geschälten Bestände erahnen. In wechselnder Intensität erstreckten sich diese auf einer Fläche von rd. 2500 ha – prozentual zusammengerechnet ergab sie eine total geschälte Fläche von ca. 600 ha (Guggenberger 1981, S.13).

Eine weitere Aufgabe der Revierleiter vor der Gründung des Nationalparks war das Führen von Jagdgästen (sowohl Forstbeamte als auch betuchte Privatleute). Die Hauptjagdzeit war während der Brunft. Vorwiegend wurde das Wild auf dem Ansitz geschossen, wenn der Abschuss noch nicht erfüllt war, kamen auch einzelne Drückjagden mit Beteiligung privater Jäger zum Einsatz (R3).

Huftiermanagement von 1970 bis 1985

Im Freestyle auf dem Weg zum Nationalpark

Als der Nationalpark Bayerischer Wald im Oktober 1970 als erster deutscher Nationalpark eröffnet wurde, gab es keine einheitlichen Vorstellungen darüber wie mit den Huftierbeständen umgegangen werden sollte. Die einen malten sich ein Wildparadies aus, in dem man riesige Rudel Hirsche auf freien Flächen beobachten könnte, die anderen forderten eine enorme Dezimierung der Wildbestände. Diese stark emotional geprägten unvereinbaren Standpunkte sind bezeichnend für die unklare Nationalparkzielsetzung der ersten Jahre (Nüßlein 1970, S.7).

Verschärft wurde dieser Konflikt noch durch die Organisationsstruktur. Auf der Fläche des heutigen Altgebietes gab es sechs Forstämter (Buchenau, Klingenbrunn, Spiegelau, St. Oswald, Mauth-West und Mauth-Ost), die 1973 im Zuge der forstlichen Gebietsreform zu einem Nationalparkforstamt zusammengefasst wurden und der damaligen Oberforstdirektion in Regensburg unterstanden. Daneben wurde, um international gültigen Standards zu entsprechen, ein Nationalparkamt mit Sitz in Spiegelau eingerichtet, welches direkt dem Landwirtschaftsministerium unterstellt war (Strunz 2010, S. 14f; J1). Für dieselbe Fläche waren folglich zwei Ämter zuständig, die jeweils eine unterschiedliche Auffassung über die Zielsetzung eines Nationalparks hatten. Das führte unweigerlich zu Spannungen, noch dazu, weil die

Kompetenz bezüglich Jagdfragen dem neu eingerichteten Nationalparkamt übertragen worden war (J4).

Der damalige Minister Eisenmann, ein großer Förderer des Nationalparks, schrieb 1973 in der AFZ: „Thema und der Inhalt unseres Nationalparks ist der naturnahe Wald mit den zahllosen Lebewesen, denen er Lebensraum und Heimat bietet". Der Gedanke eines modernen Prozessschutzes war noch wenig verankert, was folgendes Zitat des Ministers unterstreichen soll. „Die gelegentlich und besonders im Zusammenhang mit dem Nationalpark vertretene Meinung, man brauche einen Wirtschaftswald nur völlig unbeeinflusst wachsen zu lassen, um nach einigen Jahren einen Urwald vorzufinden, ist irrig. Das Umformen des Waldes in einen naturnahen Zustand ist nur durch zielbewusste Steuerung der Waldentwicklung – also durch Pflegeeingriffe – möglich" (Eisenmann 1973, S.391).

Das waldbauliche Leitbild für den Nationalpark war der standortgerechte, stabile Mischwald. „Der Grundsatz Wald vor Wild ist für den waldbaulichen Erfolg unverzichtbar […]; Maß für die angemessene Wilddichte im Nationalpark kann nur die Entwicklung der Waldjugend sein". Es wird deshalb davon ausgegangen, „dass die Schalenwildbestände so rasch wie möglich auf eine dem Äsungsangebot entsprechende Wilddichte abgesenkt und auf dieser Höhe gehalten werden" (Weinig 1973, S. 393f).

Grundlage für das Wildtiermanagement war die These, dass „die natürliche Ernährungskapazität des Nationalparks dem Bergwald entsprechend begrenzt" ist und dass auch deshalb in urwaldähnlichen Bergwaldungen anderer Regionen die Wildbestände gering sind (Nüßlein 1970, S.7). Wotschikowsky schrieb 1974 in der Zeitschrift Nationalpark: „Die Pflanzenwelt im Inneren Bayerischen Wald (also auch im Nationalpark) ist an geringe Bestände großer Pflanzenfresser angepasst, die überwiegend nur während der Sommermonate im Wald leben". Die „aus den Fugen" geratene Wechselbeziehung Wald-Wild sollte wieder ins Gleichgewicht gebracht werden (Wotschikowsky 1974a, S. 8).

Nüßlein 1970 (S. 32ff) schreibt, dass „das Erlegen und Fangen von jagdbaren Tieren im Grundsatze eingestellt wird; als Ausnahme bleibt es zur Regulierung der

Schalenwildbestände und zur Durchführung des Jagdschutzes zugelassen“. Und auch Sperber konstatiert 1973, dass die herkömmliche, auf ökonomische Ziele ausgerichtete Hege, in einem Nationalpark fehl am Platz ist und „Eingriffe in die Landschaft und in deren Tierbestand können nur unter dem Gesichtspunkt der ökologischen Ordnung erfolgen“. Es „muß eine natürliche Entwicklung der Pflanzen- und Tierwelt gewährleistet sein, Voraussetzung dafür ist die Reduktion des künstlich vermehrten Schalenwildes. Ziel der Bestandesverminderung bei Rot- und Rehwild können keine theoretischen ‘Wilddichten‘ sein. Weiser für ihre angemessene Höhe ist zum einen der Zustand der Vegetation und zum anderen die Verfassung der Tiere selbst“ (Sperber 1973, S. 400).

Über diese forstlichen Zielsetzungen hinaus, gab es keine spezifischen nationalparkbezogenen Zielsetzungen, die eine Richtschnur für das Handeln gewesen sein könnten. Auch die spätere Naturschutzgesetzdefinition war so vage formuliert, dass sich daraus kein Handlungsleitfaden ergab. Darüber hinaus waren die Nationalparkmitarbeiter vor allem damit beschäftigt, aktuelle Probleme zu lösen, so dass kaum Zeit für konzeptionelle Arbeit blieb.

Die Nationalpark-Pioniere waren selbst auch „Anfänger, die zwar eine Grundidee von dieser Aufgabe hatten, aber im Grunde auch erst mit der beginnenden Entwicklung und der wachsenden Erfahrung lernen mußten, was ein Nationalpark hier überhaupt werden soll und sein kann“ (Burger 1990, S. 4). Schon wenige Jahre später benennt Ulrich Wotschikowsky – selbst ein Nationalpark-Pionier - das Dilemma Schalenwildregulierung in Nationalparks: „Eingriffe sind in Nationalparks grundsätzlich nicht üblich. Vorrangig ist hier die ungestörte Entfaltung der natürlichen Kräfte.“ Diese Prämisse müsse dort modifiziert werden, wo aufgrund fehlender Regulationsmechanismen ernste Veränderungen des Öko-systems zu befürchten wären. „In den Lebensgemeinschaften mitteleuropäischer Nationalparks zwingen uns der Verlust des Raubwildes und der Überwinterungsmöglichkeiten für den Rothirsch –so er vorkommt – zu solchen Eingriffen.“ Bei selbigen solle jedoch immer die Erhaltung der Wildtiere in freier Wildbahn, sowie deren natürliche Verhaltensweisen berücksichtigt werden. Nicht nur deshalb sei „Jagd nur ein sehr mangelhafter, wenn nicht untauglicher Ersatz für verlorengegangene Regulationsmechanismen. Die Gefahr einer negativen Auslese ist immer gegeben“ (Wotschikowsky 1974c, S.17ff).

Damit wurde im Nationalpark eine Abkehr von der jagdlichen Hege vollzogen. Ein gutes Beispiel dafür war die Einstellung der Trophäenjagd. (NPV-BW (Hrsg.) 1995, S.VII.1-43f): „Seit seiner Gründung findet im Nationalpark keine Erlegung von Trophäenträgern mehr statt.“ „Jagdgäste gibt es nicht.“ (Buchli et al.1981, S.33f) Thiele vermerkt 1987 rückblickend: „Es werden keine erwachsenen Rebböcke und keine Hirsche, die älter als drei Jahre sind geschossen; dieser Teil der Population spielt für die Bestandesentwicklung keine Rolle. Außerdem wollte man sich von vornherein nicht dem Vorwurf der Trophäenjagd aussetzen“ (Thiele 1987, S.79). Die Regulierung war damit Dienstaufgabe, der im Nationalpark tätigen Personen. Zeitzeugen berichten, dass anfangs von der Regelung nur das Rotwild berührt war, „beim Rehwild hat das länger gedauert“; etwa ab den 1980er Jahren galt dann die Bestimmung, dass bei den männlichen Rehen nur Jährlinge erlegt werden dürfen (R3).

Der Wald und die Minimierung der „gigantischen“ Schäl- und Verbissschäden hatten Priorität für das Handeln der Verwaltung. Es wurde „energisch“ alles getan, um die Wildbestände zu reduzieren. Die Fütterungen standen in enger Beziehung zu den Schälproblemen, deshalb „weg mit den Fütterungen, so schnell wie möglich“ und „den Abschuss so weit wie möglich hochschrauben“ – auch gegen den Widerstand von Mitarbeitern des Nationalparkforstamtes. Eine „vernünftige“ Gestaltung der Jagd wurde postuliert; man sollte die „Jagd einstellen und von Wildbestandesregulierung sprechen“ (J1). Gejagt wurde in den Anfangsjahren des Nationalparks innerhalb der gesetzlichen Jagdzeit und auf ganzer Fläche, auch im Hochlagenfichtenwald – dieser war damals sehr licht bewaldet und moosreich, also ideal zum Pirschen (J1). Ein anderer Zeitzeuge erzählte, selten in den Hochlagen gejagt zu haben, da die Bergung schwierig gewesen sei (R4). Die Diskussion, Flächen ‘jagdfrei‘ zu machen, sei schon im Gange gewesen, aber bis Ende der 1970er Jahre nicht realisiert worden (J4).

Rothirschmanagment

Im Gründungsjahr des Nationalparks erreichte der geschätzte Winterbestand des Rotwildes ca. 500 – 600 Tiere (evtl. sogar Unterschätzung aufgrund der schwierigen Beobactungsverhältnisse) (Wotschikowsky 1974a, S.8). Aufgabe der beim Nationalparkamt angestellten Berufsjäger war die Zählung der Rothirsche an den Fütterungen im ersten Winter mit einem Ergebnis von gar 600 – 700 Stück Rotwild auf der Fläche des heutigen Altgebietes (B2). Auch ein ehemaliger Revierleiter schätzt die Ausgangslage auf ca. 4,5 – 5 Stück/100 ha (R3). An Heiligabend 1971, zur besten Sendezeit, strahlte die ARD Horst Sterns „Bemerkungen über den Rothirsch“ aus – Anlass und Schauplatz für diesen folgenschweren Dokumentarfilm war die Situation der Rothirsche im Nationalpark Bayerischer Wald (Sperber 1989, S. 6f).

Natürliche Verluste spielen – im Gegensatz zu den Rehen kaum eine Rolle; das Rotwild unterliegt voll der menschlichen Bestandesregulierung (Wotsch 1981, S.87). Im Winter 1972/73 wurde im Nationalpark ein Bestand von 380 Stück Rotwild ermittelt (Wotschikowsky 1973, S.402). Die „Herstellung ursprünglicher Bestandeshöhen und –strukturen“, die „Erhaltung und Wiederherstellung natürlicher Lebensgemeinschaften“ sowie die „Unterbindung des Einflusses auf die Vegetation während der nahrungsarmen Zeit“ waren Vorgaben für das Rotwildmanagement (Wotschikowsky 1973, S.402).

„Im Nationalpark wurde die Regulierung des Rotwildes energisch in Angriff genommen. Der Schwerpunkt des Abschusses lag eindeutig beim Kahlwild“ (Wotschikowsky 1978, S. 303). Obwohl es keine klaren Zielbestandeszahlen gab, strebte man „unter der Hand einen Winterbestand von etwa 1 Stück/ 100 ha an, also ca. 130-140 Stück“ (J4). Auch andere Befragte sprechen von „scharfem Jagddruck in den ersten zehn Jahren“ und einem Zielbestand zwischen 1,5 – 1 Stück/ 100 ha. „Wenn man den Bestand reduzieren will, muss man ins weibliche Wild eingreifen, das haben wir getan“ (B2). Orientiert hat man sich an der gesetzlichen Schusszeit im Jagdrecht und man hat „geschaut zu erwischen, was man erwischen kann und wenn es erkennbar war, dass der Abschussplan leicht erfüllt wird, konnte man auch noch was drauflegen“ – die Flexibilität war also hoch (J1).

Ein neuartiges Konstrukt zur Überwinterung des Rotwildes, mit dem man besonders letzteres zu minimieren versuchte, war das Wintergatter (Guggenberger 1981, S.4f). Dadurch sollten die Schäl- und Verbissschäden verhindert bzw. räumlich konzentriert und begrenzt werden (R3). Zudem wollte man damit die winterliche Auswanderung der Tiere simulieren und Schäden in den Privatjagdrevieren außerhalb vermeiden. In der Zeit von 1970 bis 1974 wurden drei solcher Fütterungsgatter angelegt (StMELF (Hrsg.) 1975, S.17). Das Wintergatter Neuhüttenwiese war das erste und ist bereits im Winter 1970 in Betrieb genommen worden (B2; J1). Es hatte eine Größe von ca. 22,0 ha (Guggenberger 1981, S.4f) (damals rd. 10 ha kleiner als heute) und wurde am Standort einer alten Fütterung südwestlich der Rachel-Diensthütte errichtet (B2). Das Gatter Riedlhäng, 1972/73 im Südosten des Nationalparks bei Mauth gebaut (J1; R4; B2), war ebenfalls eine ehemalige freie Fütterung, wobei die Fütterung im Gatter aus Anfahrtsgründen um ca. 200m verlegt worden ist.(B2). Mit 41,6 ha war es beinah doppelt so groß wie Neuhüttenwiese (Guggenberger 1981, S.4f). 1974/75 wurde schließlich das Wintergatter Teufelsberg bei Neuschönau in Betrieb genommen (J4; B2). Im Gegensatz zu den beiden anderen Gattern hat man den Standort anhand einer Klimakarte ausgewählt und bewusst wärmere Lagen bevorzugt. „Man hat große Drückjagden rund um Altschönau gemacht und den Gatterbestand so auf rd. 25 Tiere reduziert“ (B2); die Rückkehrrate von Hirschen in das Gatter Teufelsberg war aufgrund dieser Störungen und private Fütterungen in der Nähe stark schwankend, zudem kam es zu Verkehrsunfällen auf der Nationalparkbasisstraße (Wotschikowsky 1981, S.90f). Damit erschien eine weitere Betreibung des Gatters nicht mehr sinnvoll und 1985 wurde es dann tatsächlich aufgelöst (Hack 1988, S.6f).

„Die übrigen Rotwildfütterungen wurden bis Winter 1974/75 vollständig aufgelassen“ (StMELF (Hrsg.) 1975, S. 17). Durch gezielte Beunruhigungen und erhöhten Jagddruck in den alten Einständen, in Verbindung mit großzügig ausgeschiedenen Jagdruhebereichen um die Gatter herum - ein Treiben in die Gatter hinein wurde nicht praktiziert - gelang die Umstellung von den freien Fütterungen auf die Wintergatter innerhalb von wenigen Jahren (Wotschikowsky 1981, S.90f). Um das Rotwild in den Gattern zudem vor Störungen durch Besucher zu schützen, wurde 1981 die „Verordnung über die Wildschutzgebiete ‚Riedlhäng‘ und ‚Neuhüttenwiese‘ im Nationalpark Bayerischer Wald“ erlassen. Eine Einschränkung des freien

Betretungsrechts innerhalb der ausgewiesenen Gebiete vom 01.12 bis 16.05. sollte dies sicherstellen.

Wichtig war die Überzeugung, dass „die Wintergatter nur voll wirksam sind, wenn sich das gesamte Rotwild während der gesamten nahrungsarmen Zeit darin befindet“ (Wotschikowsky 1973, S. 402). Deshalb wurde der Bestand außerhalb des Gatters verstärkt bejagt; „Jagdmethode war, was nicht im Gatter ist, wird erschossen“ (R3). Konkret hieß das Einzel- wie Sammelansitze, Drückjagden mit und ohne Kreisen v.a. rund um die ehemaligen Fütterungseinstände, mit dem Ziel, dass die Tiere zügig in die Wintergatter ziehen sollten. „Es war ein ständiger Wettbewerb, wer die meisten Stück schießt; Pirschbezirke gab es nicht“ (J4; R3). Jahreszeitliche Schwerpunkte waren Herbst und Frühwinter nach der Brunft und bei Schnee (B2).

Schon von Beginn an, war das Verhältnis zu den Wintergattern, auch in der Nationalparkverwaltung, sehr ambivalent. Unter dem Gesichtspunkt, dass „an ein Ziehenlassen des Wildes ins Vorland wegen der Gefährdung der dortigen Wälder nicht gedacht werden kann“ und die bisherige Winterfütterung Frühjahrsverbiss nicht verhindert, ist mit der Wintergatterung ein ausreichender Schutz der Vegetation trotz hoher Wildbestände möglich (Wotschikowsky 1973, S.402f). Neben der „Atempause für den Wald“ ermöglichen die Wintergatter eine „ziemlich genaue Erfassung des Rotwildes nach Zahl und Struktur“ (Wotschikowsky 1978, S.304f). Besonders aus Sicht der Wildtiere wird jedoch eingewendet, dass sich die Gatter an ursprünglichen klimatischen Winterausschlussgebieten für die Rothirsche befinden oder dass sie relativ klein sind und möglicherweise die sozialen Rudelstrukturen stören könnten. Des Weiteren handelt es sich immer noch um eine künstliche Fütterung, stellt einen massiven Eingriff in das artgemäße Verhalten des Wildtieres dar und ist ein Schritt hin zur Domestikation. Die Eingatterung in einem Nationalpark erscheint absurd. „Im Interesse des Wildtieres allerdings kann dies kaum als Dauerlösung angesehen werden“ (Wotschikowsky 1973, S.402f). „Wir hatten die Ansicht, die Wintergatter seien eine vorübergehende Lösung; das war damals schon vollkommen im Widerspruch zu einer Nationalpark-Zielsetzung. […] Zur Entlastung des Waldes wollte man die Hirsche konzentrieren und an einer Lösung arbeiten“ (J4). „Trotz der erkennbaren günstigen Wirkung auf Vegetationsentwicklung und Lebensgemeinschaften kann die ‚Lösung‘ des Rotwildproblems durch Eingatterung während des Winterhalbjahres auf die Dauer nicht befriedigen“ (StMELF (Hrsg.) 1975, S.20). „Die Wintergatterung während der kalten Jahreszeit (somit das halbe Leben lang!) ist ein bedauerlicher Kompromiss zugunsten hoher Wildbestände und nur in zweiter Linie als allerdings fragwürdiger Ersatz für fehlende Wintereinstände zu sehen“(Wotschikowsky 1974a, S.9). Die Meinungen über die Gatter waren auch innerhalb der eigenen Verwaltung gespalten: „Man wollte das Rotwild wie in einer Kaserne da festmachen und füttern wie man will. Es war natürlich auch eine Attraktion, da gab es eine große beheizte Besucherkanzel [Riedlhäng] und einmal pro Woche Führungen“ (R4).

Ein Problem, das der flächige, scharfe Jagddruck mit sich brachte, war die zeitlich und räumlich ungleichmäßige Verteilung der Rothirsche. Der Grenzstreifen auf tschechischem Gebiet spielte dabei als Sommerlebensraum und Rückzugsgebiet eine entscheidende Rolle – „wie ein Eldorado“ (R3); „der Nationalpark war praktisch das ganze Sommerhalbjahr rotwildfrei“ (B1). „Zur Zeit der Reduktionswelle auf bayerischer Seite hatte der Grenzstreifen eine große Bedeutung, denn die Hirsche sind im Frühjahr auf direktem Weg aus den Gattern in die Hochlagen innerhalb des Grenzstreifens gezogen, dort herrschte den Sommer über Jagdruhe und nach der Brunft zogen sie direkt wieder in Gatter; wir hatten also keine Möglichkeit der Bejagung“ (J3). Auch Buchli & Voser 1981 beschreiben dieses tradierte Verhalten der Tiere und weisen darauf hin, dass dadurch der Lebensraum nicht entsprechend der Kapazität genutzt wird und die Bejagung erschwert ist; „das ‚Standwild‘ ohne Wandertradition wurde fast ausgerottet, die ‚Pendler‘ hingegen konnten sich ungestört vermehren und die Tradition weitergeben“.

Ziel sollte deshalb sein, den Bestand besser auf den gesamten Lebensraum zu verteilen und die Wildschäden auf ein Minimum zu senken. Sie machen den Vorschlag, den Populationsteil mit Wandertradition deshalb stärker zu bejagen, um die Standwildtradition zu fördern (Buchli & Voser 1981, S. 12ff, 39). „Erst im Herbst lässt sich also eine quantitativ wirksame Abschußtätigkeit […] durchführen“, obwohl dann – gemessen an den Äsungsmöglichkeiten – das Rotwild im Wintergatter sein müsste (Wotschikowsky 1973, S.403). Bereits damals kam es zur Forderung nach einer „Regulationsmethode, die für das Wild mit geringstmöglicher Beunruhigung verbunden ist“ (Wotschikowsky 1974a, S. 8); „so muß die Regulation so vollzogen werden, daß das Wild vom Druck der Angst vor dem Menschen weitgehend entlastet wird“ (Wotschikowsky 1973, S.403), nicht zuletzt, damit die Besucher den gewünschten „Nationalpark-Effekt“ erleben und vielleicht freilebendes Rotwild beobachten können. „Das allerdings würde eine Änderung bisher geübter Jagdmethoden erfordern“, sowie ein Wegegebot auf Teilflächen (Sperber 1973, S.401).

Was Herr Dr. Sperber damit gemeint haben könnte, ist der Abschuss von Rotwild im Wintergatter und auch Wotschikowsky spricht dieses Thema offen an: „Einen Vorteil haben Wintergatter allerdings: Hier könnte überzähliges, schlecht entwickeltes oder krankes Wild auf humane Weise und ohne Beunruhigung der anderen Tiere in wenigen Tagen gefangen und getötet werden. Den Rest des Jahres wäre das Wild frei von Streß!“ (Wotschikowsky 1974a, S.9). Diese im Konjunktiv beschriebene Möglichkeit hatte man längst getestet. „Damals hat es überhaupt keine Rechtsgrundlage gegeben - die Wintergatter waren im rechtsfreien Raum; es gab keine Definition im Jagdrecht von Wintergattern und auch keine Regelung zum Abschuss im Wintergatter, das hat man einfach gemacht! Erst das Gatter und dann das Gesetz – aber das war mit dem Nationalpark das Gleiche. Später ist das dann rechtlich definiert worden und dann ist auch die Einschränkung gekommen, dass der Abschuss einer Genehmigung bedarf. Ein anderer Zeitzeuge erzählt: „Wir haben damals mit dem Abschuss im Wintergatter angefangen, wenn wir noch ein paar Stücke gebraucht haben; das war kein nennenswerter Beitrag zum Abschussplan. Der Berufsjäger machte das professionell wie kein Zweiter, da brauchte es Jäger und zwar die guten Jäger. Eine offizielle Genehmigung gab es noch nicht, lediglich die Erlaubnis, krankes Wild zu erlegen“ (J4). Gegen einen begrenzten Abschuß in Gattern dieser Größe durch besonnene, versierte Schützen können aus sachlichen Gründen keine ernsthaften Einwände vorgebracht werden. Damit soll jedoch einer Regulation größeren Stils im Gatter nicht das Wort geredet werden.“ Im Jahr 1978 wurde nach Art. 31 BayJG die Jagd auf Schalenwild in Wintergattern untersagt, wobei Ausnahmen zugelassen werden können (Wotschikowsky 1981, S.88).

„Derzeit ist die Rotwildsituation im Nationalpark trotz hoher Aufwendungen ungelöst und untragbar. […] Die Lösung des Rotwildproblems liegt zu einem wesentlichen Teil außerhalb des Nationalparks!“ (Wotschikowsky 1974a, S.12). Ein wichtiger Schritt war die Gründung des Rotwildrings Bayerischer Wald 1968. Damit waren die organisatorischen Schwierigkeiten beseitigt, die einer großräumigen Rotwildhege und –regulierung bisher entgegengestanden hatten. „Bestandeszählung und Abschussplanung wurden fortan gemeinsam und unter voller Berücksichtigung der Wanderbewegungen durchgeführt“ (Wotschikowsky 1981, S.26). Anfangs hat man die Bestände mit gewissen Unschärfen und Unterschätzungen an den Fütterungen gezählt, später in den Wintergattern an mehreren Zählterminen. Erfasst wurden der Bestand, Zuwachs (90% von Alt-und Schmaltieren berechnet), der Ort sowie die Größe des Gebietes (J1; B2). Das Geschlechterverhältnis war zugunsten des weiblichen Wildes verschoben. „Wir wollten einen Abschussplan, wo wir nicht nur den Zuwachs schießen, sondern reduzieren; also besonders viel weibliches Wild (ca. 80%) und keine Hirsche über drei Jahre. […] Die Abschussplanerstellung war am Anfang eine wahnsinnige Streiterei“ (J4). „Das ist eine reine Rechenaufgabe und hat mit der Praxis wenig zu tun“ (R3). Festgelegt war schlussendlich die Stückzahl, das Geschlecht und das grobe Alter (Hirsche, Alttiere, Schmaltiere, Kälber) verteilt auf die einzelnen Forstreviere.

Rehwildmanagement

Die Schätzungen des Frühjahrsbestandes zum Zeitpunkt der Parkgründung reichen von 600 bis 2760 Tieren (Schröder, J. et al. 1988, S.10, 34). Ähnlich den Rothirschen profitierten sie wahrscheinlich von der intensiven Fütterung und dem Fehlen der großen Beutegreifern; zudem schufen Kahlschläge und Walderschließungsmaßnahmen ‘rehfreundliche‘ Lebensräume (StEMLF (Hrsg.) 1975, S.20).

Bestandesschätzungen, die über die Markierung von Tieren, Beobachtung und anschließender Berechnung mit dem Lincoln-Index im Nationalpark durchgeführt worden waren, ergaben 1975 einen Frühjahrsbestand von 540 Rehen und 1976 wie 1977 von 420 Rehen. Es scheint sicher zu sein, dass der Bestand vor 1975 höher gewesen sein muss – die Jagdstrecken deuten darauf hin. „Ab 1975 wurden die Abschußquoten bewusst reduziert; trotzdem spricht nichts für ein Wiederanwachsen des Bestandes.[…] Für einen Nationalpark ist die Frage, welche Faktoren den Rehwildbestand letzten Endes entscheidend regulieren, von zentraler Bedeutung. Sie ist ohne konkrete Vorstellungen über die Anzahl der Rehe kaum befriedigend zu beantworten. Doch die Ermittlung brauchbarer Rehbestandeszahlen ist in Waldrevieren ein ungelöstes Problem“ (Wotschikowsky 1981, S.74ff).

Das Ziel in den ersten Jahren des Nationalparks war, „so viele Rehe wie möglich schießen“. Bezüglich des Abschussplanes „hat man geplant, was man glaubte erlegen zu können; festgelegt wurde Stückzahl, Alter und Geschlecht“ (J1)“. Die anfänglich hohen Abschusszahlen führten auch zu Diskussionen mit der Oberforstdirektion in Regensburg, die die Pläne genehmigen musste (J4). Der Abschuss wurde dann auf die einzelnen Reviere verteilt, wobei man diese Zuteilungen oft nicht derart realisieren konnte. Reduzieren wollte man die Rehe wegen des Verjüngungszustandes (R3). Ziel war, v.a. den Abschuss der weiblichen Rehe zu erhöhen. Das Motto war ‘Zahl vor Wahl‘ und die Flexibilität bezüglich des Abschussplanes war hoch, wobei alle erlegten Tiere richtig verbucht wurden (B2).

Die größte Rolle bei der Bejagung der Rehe spielte der Einzelansitz, auch Sammelansitze und Autopirsch waren üblich (J4; J1; R3; B2). Drückjagden zielten eigentlich auf das Rotwild ab, Rehe waren hier eher „Zufallsergebnisse“ (J1; J4).

Der überwiegende Teil der Rehwildfütterungen wurde ebenfalls in den 1970er Jahren aufgelöst, 10 Anfang bis Mitte der 1980er Jahre und die letzten drei 1990. Die Forschung unterhielt einzelne kleine Futterplätze zum Rehfang Mitte der 1980er Jahre. Im Nachhinein stellte sich offenbar heraus, dass die Einschränkung der Winterfütterung zur Reduzierung des Rehwildbestandes effektiver war als der hohe Abschuss, da die Tiere entweder ins Vorfeld abwanderten oder der natürlichen Selektion des Winters zum Opfer fielen. Auch Wotschikowsky (1978, S.305)kommt zum gleichen Schluss. Die „starke Einschränkung der Rehwildfütterung“ zusammen mit der Wintergatterung des Rotwildes hat sich sehr günstig auf die Vegetation ausgewirkt. Seit Anfang der 1980er Jahre wird die Bejagung der Rehe als ‘sehr zurückhaltend‘ bezeichnet (Hack 1988, S.6ff). Es gab in dieser Zeit auch schon die Überlegung, keine Rehe mehr zu schießen, mit der Begründung, dass sie frei wandern könnten und wegen der hohen Schneelage nur einen geringen Einfluss auf die Vegetation hätten (J1; J4). Zudem hoffte man darauf, dass „die Rehe von den Nachbarn effektiv bejagt werden“ (J4; vgl. auch Buchli & Voser 1981, S.40).

Huftiermanagement von 1986 - 1997

Effektive Methoden und Rückzug aus der Fläche

Allgemeine Grundsätze und Ziele 1986 – 1997

Die Gründerjahre sind vorbei. […]Das nächste Jahrzehnt wird ein Jahrzehnt der Stabilisierung und Bewährung sein“ (Bibelriether 1980, S.8). Die wilden Zeiten und der Freistil der Anfangsjahre scheinen gezähmt und ein Zeitzeuge meint dazu scherzend: „Eigentlich ist das ein Wunder, dass wir das überlebt haben“ (B2). Bezüglich der groben Leitlinien wird die Richtung der frühen 1980er Jahre beibehalten, Änderungen betreffen vor allem das WIE, also die Umsetzung.

Sperber plädiert 1987 dafür, die „Wildbestände im Nationalpark so lange zu reduzieren, bis sich die Bodenvegetation vollständig regeneriert hat“. Die unerlässliche Regulierung von Schalenwildarten sei so vorzunehmen, dass Tierwelt und Besucher nur minimal gestört würden. Er schlägt effektive Gemeinschaftsjagden und die örtliche und zeitliche Beschränkung der Eingriffe vor; und er geht noch einen Schritt weiter, indem er verlangt, die „Fangjagd künftig auf das Schalenwild zu verlagern“ – also Rotwild im Wintergatter, Schwarzwild im Saufang und Rehe mittels Kastenfallen zu regulieren. Des Weiteren seien „faunenfremde Objekte jägerischer Hege, wie Dam-, Muffel- und Sikawild […] in Nationalparks nicht zu dulden (Sperber 1987, S. 39f). Auch Thiele postuliert „neue Regulationsmethoden für Reh- und Rotwild, um Wald und Wild ins Gleichgewicht zu bringen“, stellt aber auch fest, dass sich die Bodenvegetation bereits erholt hätte (Thiele 1987, S. 78f). Ein Befragter schildert die Situation so: „Aufgrund der Abgrenzungsdefizite – der Nationalpark ist hauptsächlich Sommerlebensraum – aber auch der Defizite, die in der Ausrottung der Großraubtiere im Gebiet bestehen und der Einflüsse, die von außen auf das Parkgebiet einwirken, wurde von Beginn an die Notwendigkeit gesehen, die Schalenwildarten zu managen und so einen Ausgleich herzustellen zwischen den Interessen des Naturschutzes und den Belangen der Bevölkerung außerhalb.“

Wichtige Meilensteine in dieser Zeitperiode waren die rechtliche Absicherung des Abschusses im Wintergatter und die Einstellung der Rehjagd im Ostteil des Nationalparks im Jahr 1986. Um die Jagd effektiver zu gestalten, hat man ab 1987 die Schonzeit bis 31.08. verlängert und vermehrt Drückjagden durchgeführt (Hack 1988, S.7f; R1). Gleichzeitig wurde die bejagte Fläche reduziert. Vieles deutet darauf hin, dass dies sukzessive passiert ist; bezüglich der Flächengröße und des Zeitraumes gibt es jedoch differierende Aussagen. Ein Revierleiter erinnert sich, dass ab 1981 in der sog. Reservatszone kein Schuss mehr gefallen sei und dass sich die Jagd auf die unteren Flächen reduziert habe. Thiele konstatiert 1987, dass es auf rd. 50% der Fläche keine Eingriffe mehr gäbe (Thiele 1987, S.78f). Thor dagegen schreibt 1988, dass ca. ein Drittel der gesamten Nationalparkfläche Schutzgebiet sei, in dem weder Jagd noch Holzwirtschaft betrieben würde (Thor 1988, S.14). Sicher ist, dass im März 1987 die erste Fassung der 'Verordnung über die Einschränkung des Betretungsrechts im Nationalpark Bayerischer Wald' in Kraft trat. In dieser Verordnung ist erstmals von einem 'Kerngebiet' die Rede, in dem man die markierten Wege nicht verlassen darf, u.a. um das Reh- und Rotwild in ihren Einständen nicht zu beunruhigen und so „Folgeschäden durch Verbiss und Schälen" hervorzurufen. „Die Vorbereitung und Durchführung der Aufgaben der Nationalparkverwaltung" sind u.a. von dem Verbot ausgenommen. Dieses Kerngebiet steht jedoch nicht in direktem Zusammenhang mit einer Zonierung (Strunz 1993, S.22). Trotzdem fand nach Angaben von Befragten innerhalb dieses Gebietes keine Jagd mehr statt (J3; B2). Anfang der 1990er Jahre war das international gültige Ziel – '75% der Fläche Naturzone ohne lenkende Eingriffe' – erreicht.

Am Ende dieser Periode wurde der Entwurf des Nationalparkplanes von 1995 ausgearbeitet. Als Grundsatz wurde hier eine „weitgehende natürliche Selbstregulation" festgeschrieben. Wo diese jedoch durch fehlende natürliche Feinde, fehlende Winterlebensräume oder Fremdbeeinflussung von außen gestört sei, müsse eingegriffen werden, denn „nachteilige Veränderungen der Waldlebensgemeinschaften durch Überweidung und Verbiss der Bodenflora und Baumverjüngung stellten den Schutzzweck des Nationalparks in Frage". Die Maßnahmen dienen ausschließlich der Bestandeskontrolle oder der wissenschaftlichen Forschung – nicht der Nutzung von Ressourcen. Sie sollen zeitlich und räumlich eingeschränkt, auf Grundlage wildbiologischer Untersuchungen und ausschließlich durch Personal der Nationalparkverwaltung erfolgen. Des Weiteren seien sie laufend auf Effizienz, Nationalpark-Verträglichkeit und Wirkungen im Waldökosystem zu überprüfen (NPV Bayerischer Wald (Hrsg.) 1995, S. VII.1-43ff).

Rotwildmanagement 1986 - 1997

„Das Rotwild hat während aller Jahreszeiten im Park abgenommen, durch die Wintergatter sind die Schälschäden bedeutungslos geworden und der Verbiss ist zurückgegangen“, stellt Wotschikowsky bereits 1981 fest. Viel wichtiger als die Bestandesregulierung sei die Umstellung von freier Fütterung hin zum Wintergatter gewesen. Er merkt an, dass der Einfluss des Rotwildes viel stärker zurückgegangen sei als der des Rehwildes (Wotschikowksy 1981, S.98f). Über zehn Jahre später findet dies im Entwurf des Nationalparkplanes von 1995 Bestätigung: „Die aktuelle Schälbelastung der Wälder ist auf ein Ausmaß zurückgegangen, dass es für die Schutzziele des Nationalparks keinerlei negative Auswirkungen mehr erwarten lässt“; insgesamt sei eine weitere leichte Verbesserung der Verbissbelastung durch die Huftiere festzustellen. Der Trend deute auf eine Stabilisierung auf niedrigem Niveau hin (NPV Bayerischer Wald (Hrsg.) 1995, S. VII.1-44ff).
„Gemittelt über den ganzen Zeitraum haben wir versucht, den Zuwachs abzuschöpfen – mit einer Abweichung von 10-20%; […] der Abschussplan wurde am Zuwachs festgemacht“. Die Zählung erfolgte zu 90% im Wintergatter. Es gibt Vermutungen, dass diese mit gewisser Unschärfe behaftet war, da möglicherweise durch den nicht ganz dichten Grenzzaun ein gewisser Austausch stattfand. Das Ziel war, den Bestand nicht weiter anwachsen zu lassen. Die Abschussplan-Vorschläge sind von der Hochwild-Hegegemeinschaft nie infrage gestellt worden und wurden bei der Erfüllung nicht als „Bibel“ betrachtet (J3).

Die entscheidende Rolle spielte dabei das Wintergatter-Management. Obwohl es eine „Störgröße in diesem Wunschsystem Nationalpark“ ist, war das Ziel, das „Rotwild so früh und so zahlreich wie möglich in die Gatter zu bringen; es sollte eine Gattertradition entstehen“. Ende November, Anfang Dezember, wenn sich dann der Großteil des Rotwildes im Gatter befand, wurde außerhalb konzentriert eingegriffen. „Interne Vorgabe war, auch möglichst viele Rothirsche außerhalb zu erlegen“ (J3). Dazu hat man im Winter regelmäßig Drückjagden und Gemeinschaftsjagden im Randbereich des Nationalparks veranstaltet (J3; R4). „Wir waren der Meinung, das ist artgerechter als mit lauten Hunden zu jagen;[…] Mehr Erfolg hatten wir aber bei der Einzeljagd und Pirsch, wobei die Hauptverantwortung bei den Berufsjägern lag“ (R1).

Neben der Jagd im Randbereich prägte diese Periode noch ein anderes Kapitel, nämlich der Gatterabschuss. 1986 erhielt man dazu die offizielle Genehmigung, wobei die Anzahl der Stücke begrenzt und eine Berichterstattung verpflichtend war. Diese Ausnahmegenehmigung wurde dann jährlich auf Einzelantrag beim Ministerium weiterverlängert. Erst mit Erlass der Nationalparkverordnung 1992 wurde der Abschuss im Wintergatter auf Dauer legalisiert (J3; B2). Auf die Frage nach der eigenen Meinung zu dieser Praxis reagierten alle Befragten dieser Periode ähnlich: Der Wintergatterabschuss bedeutet weniger Jagdstress, Jagdzeitverkürzung und mehr Handlungsmöglichkeiten. Wir erledigen unseren Rotwildabschuss innerhalb von zwei Monaten und setzen die Tiere einer maximalen Stresssituation von 20-30 Minuten aus“ (B2).
Der Ablauf einer solchen Aktion soll im Folgenden beispielhaft am Wintergatter Neuhüttenwiese, gemäß den Angaben eines Zeitzeugen, skizziert werden. Grundsätzlich bestanden damals zwei verschiedene Methoden. Zum Einen der Abschuss von Tieren direkt im Hauptgatter von einer Kanzel am Gatterkopf aus, früh morgens auf dem Weg von der Fütterung zurück. Um die ‚Schuss-Mensch-Gefahr-Verknüpfung‘ zu vermeiden, war es wichtig erst nach ca. 60 Minuten zum Anschuss zu gehen. Die zweite Methode entwickelte sich erst später und erforderte einen Anbau an das bestehende Hauptgatter in Form eines sogenannten ‚Vor- oder Nachfanggatters‘(B2). Dieses ‚Zwei-Gatter-System‘ findet auch heute noch (2011/2012) in den beiden Gattern des Altgebietes Neuhüttenwiese und Riedlhäng Anwendung und soll an dieser Stelle für beide Perioden behandelt werden, um eine Redundanz zu vermeiden. Wie oben schon erwähnt, versuchte man bis Ende November über die Fütterung den Großteil der Rothirsche ins Gatter zu bekommen; dazu wurde und wird im Hauptgatter nach der Brunft (Mitte Oktober) eine geringe Futtermenge ausgebracht und gewartet, bis sich ca. 40-50 Stück dort einfinden. Daraufhin wird das Hauptgatter geschlossen und alle Nachzügler müssen die ‚Schleuse‘ des Nachfanggatters passieren. Ziel ist, dass die Tiere im Hauptgatter ohne Stress den ganzen Winter versorgt werden und vom Abschuss nichts mitbekommen (B1; B2). „Im Nachfanggatter werden die später eintreffenden Rothirsche rudelweise über den ganzen Winter nachgefangen, entweder per Selbst-

oder Handauslösung. In der Regel fängt man abends bei Dunkelheit und weiß daher schon, wie viele im Vorfanggatter sind. Am frühen Morgen – meist zu zweit – bezieht man die beiden Hochsitze, schaut nochmal was drin ist und bestimmt, was geschossen wird“ (B1). Es bestand und besteht dann die Möglichkeit, über manuell bedienbare Tore einzelne Tiere direkt in das Hauptgatter zu schleusen, wobei Mutterfamilien nicht getrennt werden sollten (B1; B2). Zum Separieren von starken Hirschen direkt in das Hauptgatter, musste man damals noch in das Vorfanggatter hineingehen (B2). Wichtig sei es auch gewesen „komplette Familienverbände zu eliminieren, um die Erinnerung zu beseitigen“ (J3). Es sollten vorwiegend Kälber und Alttiere erlegt werden. Teilweise haben auch einige Tiere den Gatterabschuss mitbekommen. Im Lauf der Jahre wurde das Vorfanggatter wesentlich vergrößert und Bäume integriert, um Panik zu vermeiden (B2). Zum Ende dieser Periode erfolgte die Regulierung schwerpunktmäßig in den beiden Wintergattern des Nationalparks (NPV Bayerischer Wald (Hrsg.) 1998, S.13).

Rehwildmanagement 1986 - 1997

Es gab bereits schon vor 1986 Überlegungen, die Regulierung der Rehe im Nationalpark stark einzuschränken. Im Gegensatz zum Rotwild „könnte sich der Mensch als beeinflussender Faktor auf die Rehpopulation sicher problemloser zurückziehen“, schreibt Strunz 1987 in der Zeitschrift „Nationalpark. Die Nationalparkverwaltung hätte erste Schritte eingeleitet, indem sie in den rd. 80 km² umfassenden Reservatsgebieten keine Abschüsse mehr durchführe. Die Abschusshöhe sei sehr gering (unter 0,5 Stück pro 100 ha) und der Beginn der Abschusszeit würde vom 15.05. auf den 01.09. verlegt, um Störungen durch die Bejagung auf einen kürzeren Zeitraum zu beschränken. „Versuchsweise wird im Ostteil […] kein Abschuss mehr getätigt“, wovon man sich auch eine bessere Beobachtbarkeit der Tiere erhoffte (Strunz 1987, S.9).

Unter der Überschrift „Neues Konzept für die Regulierung des Rehwilds im Nationalpark Bayerischer Wald“ konkretisiert Thiele 1988 in derselben Zeitschrift das Vorhaben. Grundlage dafür seien umfangreiche Forschungsprogramme zur Bestandesentwicklung und Raumnutzung gewesen. Zudem spiele der Tannenverbiss eine Rolle; mithilfe von jährlichen Vegetationsaufnahmen solle dieser – zusätzlich zum 1986 erstmals durchgeführten ‘Forstlichen Gutachten zur Situation der Waldverjüngung erfasst werden. „Derzeit sind zwischen 40 und 50 Prozent der Tannen verbissen; […] entscheidend ist, daß ein Ziel festgelegt wird, eine bestimmte Mindestzahl von Tannen je Hektar, die für die nächste Waldgeneration zur Verfügung stehen muß“. Eine konkrete Anzahl nennt er jedoch nicht. Das Konzept sieht zwei „Regulierungsreviere mit je ca. 1200 ha“ vor, in denen Dichte und Verteilung gesteuert und der Abschuss so lange gesteigert werden soll, bis diese Mindestzahl von Tannen unverbissen bleibt. „Der Rest des Nationalparks außerhalb der Regulierungsgebiete dient als ‚0‘-Fläche“. Reguliert werde erst ab September und mit möglichst effektiven Methoden, wie „Abschuss an der Kirrung oder Drückjagden, um die Störung möglichst gering zu halten“ (Thiele 1988, S. 16f).

Bezüglich der Abschussplanung hatte und hat der Nationalpark als Untere Jagdbehörde und eigene Hegegemeinschaft die komplette Entscheidungsgewalt. Neben dem Vegetationsgutachten, einer 10-jährigen Verbissinventur oder der Anzahl an Tannen/ha, die in die nächste Altersstufe eingewachsen sind, spielten bei der Planerstellung auch die Faktoren „Luchs“ oder ein absehbarer langer harter Winter eine Rolle. Festgelegt waren die Stückzahl und das Geschlecht, wobei der Schwerpunkt mit ca. 80% auf weiblichen Rehen und Kitzen lag und die Flexibilität hoch war (J3). Es gab Pirschbezirke für Nationalpark-Mitarbeiter und man versuchte die Rehe vorwiegend über die Kirrjagd und mit Sammelansitzen zu erlegen (J3; R1).

Huftiermanagement von 1998 bis 2012

Das Ende des Rehwildmanagements aber die Wintergatter bleiben bestehen

Allgemeine Grundsätze und Ziele 1998 – 2011

Die ‘modernen‘ Grundsätze und Ziele für das Schalenwildmanagement orientieren sich nach der Erweiterung des Parks im Allgemeinen am rechtlichen Rahmen des novellierten Naturschutzgesetzes und im Speziellen an den Vorgaben der ebenfalls novellierten Nationalparkverordnung. Es erfolgt keine wirtschaftsbestimmte Nutzung und weder Verbiss noch geschälte Bäume sind als „Schäden“ im Nationalpark zu betrachten. Auch in Bezug auf das Schalenwild soll das Prinzip „Natur Natur sein lassen“ gelten, mit der Ausnahme, dass Eingriffe notwendig werden können, wenn Eigentumsrechte angrenzender privater Grundbesitzer oder Nationalparkziele gefährdet sind. Im Hinblick auf die beiden vorausgegangenen Perioden ist vorwegzuschicken, dass sich nicht nur die rechtlichen Rahmenbedingungen verändert haben, sondern besonders die ökologischen. Seit Mitte der 1990er Jahre wird das Bild des Nationalparks von einer Borkenkäfer-Massenvermehrung dominiert, wobei ca. 6000 ha Fichtenbestände abgestorben sind. Die Zunahme der Schlagflora und Walderneuerungsprozesse sorgen dafür, dass der Großteil der Biomasseproduktion auf dem Waldboden und somit in ‘Äserhöhe‘ stattfindet. Eine weitere Veränderung stellt die Etablierung der Luchspopulation dar und nicht zuletzt hat 1998 der Nationalparkleiter gewechselt (Heurich et al. 2009, S. 134).

Im aktuellen und gültigen Nationalparkplan, Band Schalenwildmanagement, sind die Grundsätze und Ziele formuliert und sollen an dieser Stelle kurz zusammengefasst werden. „Vorrangig“ ist die Erhaltung der Schalenwildarten in arttypischen, lebensfähigen Populationen – nicht nur als Bereicherung der Artenvielfalt, sondern vielmehr als Träger wichtiger waldökologischer Prozesse. Ein weiteres Bestreben ist die Sicherung der Biodiversität bezüglich der heimischen Flora und Fauna; ein bestandesbedrohlicher Verbiss bei Eibe und Türkenbund oder die negativen Auswirkungen auf die Rauhfußhühner beispielsweise könnten dies gefährden. Um die Pufferfunktion nach außen gegen einen Borkenkäferbefall wirksam sicherzustellen, ist eine standortheimische, mischbaumartenreiche Waldzusammensetzung im Randbereich voraussetzend; dort den selektiven Verbiss der Mischbaumarten zu verhindern, ist das dritte Ziel.

Der Schutz der an den Nationalpark angrenzenden Privatgrundstücke und der Enklaven vor Wildschäden, sowie die Sichtbarkeit und Erlebbarkeit von Wildtieren, welche aufgrund der Einschränkung der Bejagung, der Ruhezonen und dem Wegegebot heute schon zugenommen haben, sind weitere Leitbilder. Daran anknüpfend ist ein generelles Ziel, die regulativen Eingriffe weiter zu verringern (in Absprache mit der privaten Jägerschaft) und Störungen durch diese Maßnahmen, wie auch durch Besucher, zu vermeiden. Last but not least besteht die Intention, insbesondere das Rotwild-Management, sowohl mit dem Nationalpark-Vorfeld als auch mit dem Nationalpark-Šumava, abzusprechen. Mit Ausnahme des erstgenannten Ziels gibt die Reihenfolge keine Zielhierarchie vor – „bei allen Maßnahmen sind die verschiedenen Ziele des Schalenwildmanagements untereinander, sowie mit anderen Schutzzielen des Nationalparks abzuwägen“. Auf die Frage, was ihrer Ansicht nach die Ziele des Schalenwildmanagements sind, beurteilen manche Experten die Zielvorgaben eher kritisch: „Der Nationalparkplan ist so unverbindlich gehalten, dass alles möglich ist – sehr aufgebläht ohne klare Aussagen“; der Erhalt der heimischen Schalenwildarten und der Schutz der angrenzenden Grundstücke seien dabei noch am konkretesten. Die Förderung der Sichtbarkeit und Erlebbarkeit sei schwer zu realisieren aufgrund der derzeitigen Waldstruktur im Nationalpark“ (J2). Ein anderer Befragter gibt mit Hinweis auf den Anlageband Schalenwild an, dass das Hauptziel sei, die Wildart Rotwild zu erhalten. „Das Rotwild ist nicht unbedingt das Lieblingstier des Waldbesitzers, weil es eben Schäden verursachen kann und deshalb sollte der Nationalpark einen gewissen Einfluss behalten, dass das Wild als solches einen Lebensraum behält; […] der Hauptgrund, warum wir eigentlich jagen ist, dass die Außenwirkung möglichst gering ist“ (R2).

Ebenfalls auf das Rotwild bezogen räumt ein anderer ein: „Was ist unsere Zielvorstellung? Da ist sich keiner einig! Es weiß keiner, wie viele wir haben sollten oder haben dürfen oder ob der Verbiss eine Bedeutung hat oder nicht – man schwimmt irgendwie hin und her. Es gilt der Grundsatz ‚Natur Natur sein lassen‘: so wenig Jagd wie möglich und nur wo es notwendig ist und dann in einem begrenzten Zeitraum, so schnell und so störungsarm es geht“ (B1). Für ein konkretes Ziel im Nationalpark erachtet ein weiterer Experte das möglichst artgerechte Leben des Wildes in diesem Biotop. Dieses beinhalte die typische Vegetation, Äsung, Deckung, Ruhe und werde auch vom Wild selbst mitgestaltet. Die Regulation erfolge dabei aus einem Zwang heraus. „Entscheidend ist, dass sich das Wild hier wohlfühlt“ (B3). Seit einigen Jahren rückt auch das Bestreben nach sichtbarem, tagaktivem, vertrautem Wild mehr in den Vordergrund (J3; B2). Die offizielle Konzeption sieht vor, dass Eingriffe – sofern sie notwendig sind - möglichst außerhalb des Nationalparks oder auf den Randbereich verlagert (außerhalb von Kerngebiet, Natur- oder Erholungszonen in der Schalenwildmanagementzone), auf das unbedingt notwendige Maß beschränkt, möglichst störungsfrei, artgerecht und an natürliche Prozesse angepasst, durchgeführt werden.

Die Jagd wird nur von Nationalparkbediensteten ausgeführt (R2), nur in der Zeit vom 01.09. bis maximal 31.01. und ohne Ausnahme nur im Randbereich; „von gut 24.000 ha sind ca. 17.000 ha ohne Jagd“ (J2). Im Altgebiet finden auf 75% der Fläche (rd. 10.000 ha) keine jagdlichen Eingriffe mehr statt (B1) und seit 2007 gibt es dort auch keine Pirschbezirke mehr (R1). Im Erweiterungsgebiet existiert dagegen noch eine Pirschbezirksregelung. Hier zieht die Naturzonenerweiterung die Jagdruhe nach sich; „langfristig sind das noch 17% - ob es da noch Sinn macht zu regulieren, müsste man noch einmal diskutieren“ (J2).

Rotwildmanagement 1998 – 2012

Mit der Erweiterung des Nationalparks wurde das Rotwildgebiet Bayerischer Wald um ca. 4000 ha westlich von Kreuzstraßl/Falkenstein bis Bayerisch Eisenstein vergrößert (J2); damit hält der Nationalpark einen Anteil von rd. 40% am Gesamtrotwildgebiet. Im aktuellen Nationalparkplan, Band Schalenwildmanagement, wird das Oberziel ‘Erhaltung der heimischen Schalenwildarten‘ für das Rotwild insofern konkretisiert, als dass zur dauerhaften Sicherung seiner Population im Inneren Bayerischen Wald ein Frühjahrsbestand von ca. 250 Tieren im Nationalparkgebiet angestrebt wird. Relativ gesehen bedeutet das einen Bestand von etwa einem Stück / 100 ha, allerdings sollen aufgrund der sich laufend ändernden Lebensraumkapazität größere Populationsschwankungen zugelassen werden mit der Einschränkung, dass andere Schutzziele nicht beeinträchtigt werden.

Der Abschussplan für das Rotwild wird jährlich erstellt und basiert auf Zählergebnissen, die im Frühjahr (Ende Februar/Anfang März) an einem vom zuständigen Landratsamt festgesetzten Zähltermin für das gesamte Rotwildgebiet erhoben werden. Die Berufsjäger im Nationalpark zählen nicht nur an diesem einen

Termin, sondern mehrfach, um eine exaktere Zahl zu ermitteln – je kleiner das Gatter, desto genauer das Zählergebnis. Der Anteil außerhalb wird geschätzt. Diese Zählergebnisse werden an das Landratsamt gemeldet und daraufhin findet ein Treffen mit der Hochwildhegegemeinschaft, dem Nationalpark als Untere Jagdbehörde und Jagdberatern statt. Bei diesem werden die Abschussergebnisse des abgelaufenen Jagdjahres zusammengestellt, die Zählergebnisse bekanntgegeben, sowie die Vorschläge für die kommende Abschussplanung abgestimmt. Für den Nationalpark sind letztere bereits im Vorfeld mit dem Jagdleiter, den Berufsjägern und dem Nationalparkleiter getrennt für das Alt- und Erweiterungsgebiet besprochen worden. Daraufhin wird der Plan festgesetzt (J2; R2).

Die Flexibilität „vom schwachen Ende her kommend“ (R2) ist hoch, jedoch sollte die Anzahl der geplanten Hirsche nicht überschritten werden. Eine Erhöhung während der Saison ist möglich. Diese Befugnis hat der Nationalpark als Untere Jagdbehörde Es erfolgt eine Information des Leiters der Hochwildhegegemeinschaft und des Landratsamtes zur Kenntnisnahme. Die aktuelle Tendenz ist ‘leicht Reduzieren‘ (J2; B1). Ein Grund dafür ist die Bindung der Regulation an das Wintergatter; sollten mehrere milde Winter aufeinander folgen, würde ein Großteil der Rothirsche möglicherweise nicht mehr ins Gatter ziehen, der Nationalpark hätte keine Regulationsmöglichkeit mehr und die Gefahr der Schäden an den Privatjagden würde zunehmen (B1).

Rotwildmanagement im Nationalpark bedeutet Wintergattermanagement. Auch im heutigen Falkenstein-Rachel-Gebiet existierten bereits vor Nationalparkgründung zwei Wintergatter – Buchenau und Ahornschachten. Als Ausgleich für weitgehend fehlende Überwinterungsgebiete im Vorfeld des Nationalparks und aufgrund der Möglichkeit, Verbiss und Schälschäden auf den Gatterbereich zu begrenzen, sollen die vier Wintergatter bis auf Weiteres aufrechterhalten werden. Ausschließlich dort soll den Rothirschen zwischen Oktober und Mai eine Erhaltungsfütterung angeboten werden, die den natürlichen Äsungsbedingungen entspricht. In der Praxis bedeutet das Grassilage und Heu mit geringen Mengen Apfeltrester und Rüben, v.a. an der Schaufütterung (B1). Mit der Erweiterung erfolgt die Regulation in allen vier Wintergattern (NPV Bayerischer Wald (Hrsg.) 2000, S.15). Die momentane Richtung ist, den Bestand der weiblichen Tiere und des Jungwildes weiter zu senken, denn „nur so kann man den Bestand reduzieren bzw. im Griff haben und ein unbegrenztes

Anwachsen verhindern“. Es sollen möglichst ganze Familienverbände erlegt werden, keine starken Hirsche und es soll keine Selektion nach Schwächeren vorgenommen werden (J2). Ein Berufsjäger gibt an, körperlich schwache oder schlecht veranlagte Tiere eher herauszunehmen, aber eine Trophäenorientierung gäbe es nicht; „wir schauen nicht, ob der Spießer brandig ist – wenn drei drin sind, dann schieße ich sie, wobei man „früher nicht mit einem starken Hirschkalb hätte kommen dürfen“. Das Motto ‚Zahl vor Wahl‘ sei maßgeblich (B1).

An dieser Stelle muss zwischen Alt- und Erweiterungsgebiet differenziert werden, da sich die Verhältnisse (noch) unterscheiden. Es ist festzustellen, dass der Anteil des Gatterabschusses im Altpark die letzten Jahre auf über 80% gestiegen ist (B2; J2; NPV Bayerischer Wald (Hrsg.) 2008b, S.11), aber auch die Populationen in den Wintergattern Neuhüttenwiese und Riedlhäng drastisch angewachsen sind und daraufhin entsprechend eingegriffen wurde (R2).

Abbildung 5 veranschaulicht auf Grundlage der Abschussmeldungen für das Altgebiet die Entwicklung des Gatterabschusses im Verhältnis zum Abschuss außerhalb des Gatters.

Ein deutlicher Unterschied ist im Vergleich von erster zu zweiter Periode zu verzeichnen, mit einem Anstieg des Gatterabschusses von 8% auf knapp 70%. Zwischen zweiter und dritter Periode besteht eine geringe Zunahme. In Neuhüttenwiese ist das Geschlechterverhältnis aufgrund der starken Eingriffe beim Kahlwild (Absenkung von ca. 80 auf 40 Stück) mit 1:2 hin zu den männlichen Tieren verschoben. „Wir haben fast keine Schmalspießer mehr, weil die schon als Hirschkälber geschossen wurden – jetzt haben wir lauter mittelstarke und starke Hirsche“ (B2). Deshalb gibt es für dieses Gatter die Vorgabe, mehr männliche Tiere zu schießen und auch die Trophäenbegrenzung wurde gelockert, sodass für das Jagdjahr 2010/11 zehn 2er Hirsche in den Abschussplan aufgenommen wurden. Damit muss man während des Gatterabschusses nicht mehr separieren (J2).

„Die Trophäenjagd ist ein leidiges Thema mittlerweile; […] alle Trophäen müssen abgegeben werden und werden verkauft, genauso wie die Abwurfstangen; das betont, dass wir keine Trophäenjagd betrieben“ (B1). „Die Trophäenjagd ist ein Unwort im Nationalpark und ein Tabu – die klassische Trophäenjagd ist nicht unser Ziel, aber im Umkehrschluss überhaupt keine stärkeren Hirsche mehr zu schießen, weil man dann ein Tabu bricht, finde ich überzogen; […] meiner Meinung nach ist das eher eine politische Sache, dass man das damals aufgegeben hat, um das Image des Nationalparks zu stärken und weniger eine praktisch sinnvolle Sache“ (R2).

Im Falkenstein-Rachel-Gebiet macht der Gatterabschuss nur ca. 40% des Gesamtergebnisses aus (J2; NPV Bayerischer Wald (Hrsg.) 2008b, S.11) und in den dortigen Gattern (Buchenau 45,6 ha; Ahornschachten 29,2 ha) geht es vorwiegend darum, den Zuwachs abzuschöpfen (R2).

Die Wintergatterbestände sollen handhabbar bleiben – Ziel im Erweiterungsgebiet sind deshalb 60-70 Stück je Wintergatter. Das „massive Erlegen im Gatter“ kam erst mit der Nationalparkerweiterung und wird langsam gesteigert, was auch daran liegt, dass die Jagdfläche stets kleiner, der Abschuss aber gleich hoch bleibt. Im Vergleich mit der geschilderten Praxis des Gatterabschusses im Altgebiet, gibt es in den beiden Gattern des Erweiterungsgebietes leichte Unterschiede. So arbeitet man mit einem ‚Drei-Kammern-System‘ – zusätzlich zu einem Hauptgatter und einem Vorfanggatter kommt hier noch ein sogenanntes Separationsgatter zum Einsatz (R2). Wie im Altpark wird das Hauptgatter geschlossen, nachdem sich darin ein Mindestbestand eingefunden hat. Daraufhin wird sowohl im Separationsgatter als auch im Vorfanggatter gekirrt. Am Morgen wird kontrolliert und „wenn was drin ist, wird die Mannschaft zusammengetrommelt und falls ein starker Hirsch dabei ist, wird dieser separiert und je nach dem kann man im einen oder anderen kleinen Gatter schießen“. Alle Gatter sind mit automatisch schließbaren Fangtoren miteinander verbunden. „Zudem besteht die Möglichkeit bei schlechten Wintern und wenig Nachfang, einen Teil vom Hauptfang zurück ins Vorfanggatter zu locken – quasi der Umkehreffekt“(R2; B3).

Im gesamten Nationalpark wurden ab 1997 die Drückjagden eingestellt; das hatte u.a. mit dem Chefwechsel, mit der Beratung durch das Sachgebiet Forschung und nicht zuletzt mit der Tatsache zu tun, dass versehentlich in die Naturzonen hineingejagt worden war (R1). Der Abschuss außerhalb des Wintergatters spielt im Erweiterungsgebiet derzeit (noch) eine größere Rolle als im Altgebiet. Während im Altpark die Kirrjagd 2007 zusammen mit der Pirschbezirksregelung eingestellt wurde, werden im Randbereich nur vereinzelt Stücke „mitgenommen“ und die Sichtbarkeit und Vertrautheit Vorrang hat (B1), liegt der Schwerpunkt im Erweiterungsgebiet noch außerhalb der Gatter. Über Einzel-und Sammelansitze verbunden mit Kirrungen – „mit allen Problemen, die dazugehören“ – wird das Rotwild reguliert (B3).

Wie bereits erwähnt, hat man bereits Mitte der 1970er Jahre die Wintergatter nicht als Dauerzustand angesehen. Um die Thematik ‘Auflösung der Wintergatter‘ bzw. genereller zukünftiger Umgang mit dem Rotwild im Bayerischen Wald voranzutreiben, startete die Nationalparkverwaltung im Herbst 2007 das Projekt “Rothirsch auf neuen Wegen“. Es sollte einen „ergebnisoffenen, konsensorientierten Dialog“ mit den Nachbarn des Nationalparks einleiten und begleiten. Zentrales Element dieses Kommunikationsprozesses – neben öffentlichkeitswirksamen Veranstaltungen wie den ‘Hirschtagen‘ – sollte die ‘AG Rothirsch‘ werden, die aus Vertretern von Land-/Forstwirtschaft, Jagd und Naturschutz zusammengesetzt sein sollte. Die NPV wollte dabei lediglich als Moderator fungieren. Der Rothirschdialog und das Projekt sind jedoch gescheitert, eine ‘AG Rothirsch‘ kam nicht zustande. Die Gründe sind vielschichtig und über den Verlauf des Projekts sind mehrere Arbeiten veröffentlicht worden (vgl. Selter 2009, Gerner 2009, Ludwig 2009). Ein Aspekt lässt sich unter dem sog. NIMBY-Phänomen (Not In My Back Yard) subsummieren: die Akzeptanz im Allgemeinen unterscheidet sich sehr stark von der Akzeptanz der Anrainer, das heißte der direkt Betroffenen. So sei frei wanderndes Rotwild generell erstrebenswert, aber eine konkrete Gatteröffnung löse direkte Betroffenheit aus und wecke große Befürchtungen. An erster Stelle stünden die Wildschäden – aus Sicht der Waldbesitzer die Abwendung von Schäden auf den eigenen Flächen, aus Sicht der Jagdpächter die Vermeidung von Wildschadensersatzforderungen (Selter 2009, S. 29f). Als Konsequenz aus diesem Projektabbruch wird nun die Regierung von Niederbayern als zuständige Höhere Jagdbehörde ein großräumig angelegtes, gemeinsam getragenes Managementkonzept für den künftigen Umgang mit dem Rotwild im Bayerischen Wald erarbeiten. „Bis zur Fertigstellung dieses […] Konzepts wird die Nationalparkverwaltung den Betrieb der Wintergatter weiter fortführen“. Die Experten beschreiben die derzeitige Situation als „verfahren“ – man könne nicht mehr über eine Auflösung der Gatter reden (J1). Eine Lösung sei nur möglich mit Grundeigentümern und Jägern, aber „die Fronten sind verhärtet“ (J3).

Rehwild-Management 1998 – 2011

Im Gegensatz zu den Rothirschen unterliegen die Rehe im Nationalpark einer stärkeren natürlichen Dynamik – die saisonalen Wanderungen sind mit Einstellung der Winterfütterung wieder in Gang gekommen. Der winterliche Nahrungsengpass wird als natürliches Regulativ jedoch nur eingeschränkt wirksam, da in vielen

Jagdrevieren außerhalb Fütterungen betrieben werden. Zudem stellt der Luchs mittlerweile einen wichtigen natürlichen Mortalitätsfaktor dar. Der Nationalparkplan verweist auf das Ziel der Biodiversität – auf ganzer Fläche soll die Waldverüngung und die Entfaltung der krautigen Flora in ihrer natürlichen Vielfalt gesichert werden 37. Was aber versteht man unter „natürlichem Verbiss“? Ähnlich einer „natürlichen Wilddichte“ schwankt diese Größe sehr stark räumlich und zeitlich – eine Definition scheint nicht möglich zu sein (Heurich et al. 2009, S.136).

Im Rachel-Lusen-Gebiet wurde die Rehwildjagd in Absprache mit den Reviernachbarn seit 2007 eingestellt, mit Ausnahme von jährlich 10 Tieren, die für die Umweltprobenbank in Trier im Mai/Juni erlegt werden (B1). Auch im Nationalpark Šumava werden Rehe (Stand 2009) nicht bejagt (Heurich et al. 2009, S.142). Im Falkenstein-Rachel-Gebiet findet dagegen noch eine Regulation des Rehwildes statt. Es geht darum zu untersuchen, ob die Auswirkungen auf den Verbiss von Mischbaumarten im Altgebiet stärker als im Erweiterungsgebiet sind. Die Einstellung der Rehjagd soll auch den Jagdpächtern eine Kompensation der Luchsrisse in ihren Revieren signalisieren.

Auf der anderen Seite werden im Falkenstein-Rachel-Gebiet bis ca. 2020 jährlich rd. 40.000 Buchenwildlinge ohne Schutz gepflanzt und um den Erfolg dieser Maßnahmen zu gewährleisten, wird die Bejagung dort fortgeführt (NPV Bayerischer Wald (Hrsg.) 2008c, S.1f; J2; R2).

Gerade bei Anwesenheit des Luchses, in Konkurrenz zum Rotwild und bei suboptimalen Lebensbedingungen in einem reinen Waldgebiet spielt das Rehwild im Inneren Bayerischen Wald eine untergeordnete Rolle. Das spiegelt sich auch bei der 3-jährigen Abschussplanung wider – „es gibt keine so richtig guten Grundlagen“ (J2). Auf der einen Seite möchte man Mischbaumarten besonders im Randbereich haben, auf der anderen Seite weiß man aber nicht, wie man den Verbiss bewerten soll. Die Rehe im Erweiterungsgebiet wurden vorwiegend auf Sammelansitzen an Kirrungen erlegt (J2). Daneben gibt es Kirrungen an den Rehfallen im Nationalpark, „die einer eingeschränkten Fütterung gleichkommen“ (B1); andere sprechen mokant von ‘Rehfallenfütterungen‘. „Forschungseinrichtungen sind eigentlich temporär, aber wenn an einer Rehfalle von Oktober bis März Futter liegt, kanns schon sein, dass da von Oktober bis März Rehe und Hirsche stehen“ (J2). „Auf der einen Seite fahren wir die Jagd runter, auf der anderen Seite wird die Forschung intensiviert – das ist auch ein Eingriff! […] Diejenigen, die in der Forschung Rehe besendern, sollten nicht über die schimpfen, die Rehe bejagen, sondern an einem Strang ziehen“ (R2). Auf Basis der Forschungsergebnisse des Reh-Luchsprojektes wurde mit dem Jagdjahr 2012/2013 die Rehjagt im Nationalpark komplett eingestellt. Auch Abschüsse für die Forschung finden nicht mehr statt.

Fazit

Es gibt mehrere – meist nationalparkinterne – Darstellungen über das frühe Schalenwildmanagement. Dass damals die ‘überhöhten‘ Wildbestände reduziert wurden, war bekannt. Erkenntnisreich war die Motivation, die dahinterstand: Man wollte den fichtenreichen Wirtschaftsforst aktiv umbauen hin zu einem naturnahen, stabilen Mischwald und dazu brauchte man die Naturverjüngung. Lange vor der Gründung des ÖJV47 jagte man im Nationalpark also schon ‘ökologisch‘. Diese Prägung lag nicht zuletzt an dem forstlichen Personal der Nationalparkverwaltung. Der Einfluss des Wildes auf die Vegetation stellte immer einen primären Grund für die Regulation dar und tut es bis heute. Großen Wert hat man gleich zu Beginn auf das WIE gelegt: Reduzieren bedeutete starke Eingriffe ins weibliche Wild und anstelle von Hege sollte Regulation treten, was mit der Einstellung der Trophäenjagd und dem Führen von Jagdgästen verdeutlicht werden sollte. Auffällig und diskussionswürdig ist auch, dass im Vergleich zu den theoretischen Überlegungen, das Wildtiermanagement ‘nationalparkkonformer‘ zu machen, eine relativ langsame und verzögerte Umsetzung stattfand. Zum Beispiel gab es bereits Anfang der 1970er Jahre die Gedanken, dass das Ziel eines Nationalparks auch die Erhaltung der Wildtiere und deren natürlicher Verhaltensweisen sein sollte, dass die Jagd ein mangelhafter Ersatz für verloren gegangene Regulationsmechanismen sei und dass man deshalb Flächen jagdfrei machen solle – eine Schonzeitverlängerung und die Kerngebietsverordnung hat man dagegen erst 1987 auf den Weg gebracht. Ein anderes Beispiel ist das Thema ‘Wintergatterauflösung‘: schon mit ihrer Errichtung war die Haltung dazu zwiespältig und kritisch und man hat sie nicht als Dauerlösung konzipiert, sondern als Notlösung, um den Wald zu entlasten – mittlerweile ist das gesamte Rothirschmanagement darauf ausgerichtet. Obwohl die Wintergatter so konträr und befremdlich in einem Nationalpark erscheinen, geschah der erste ernsthafte Versuch sie aufzulösen erst 2007.

Beinahe genauso lange ist die Rede von einer Aussetzung der Rehwildbejagung, da man schon früh einen reduzierenden Effekt der künstlichen Regulierung bezweifelt hat. Obwohl der relative Rehwildabschuss im Vergleich zum bayerischen Durchschnitt von rd. 4 Rehen / 100 ha im Nationalpark mit gemittelt 0,7 Rehen / 100 ha und aktuell etwa 0,4 Rehen / 100 ha äußerst gering erscheint, wurde die Rehjagd im Nationalpark erst mit dem Jagdjahr 2012/2012 eingestellt.

Anders stellt sich der Vergleich der Rotwildstrecke des Nationalparks mit der relativen Strecke des gesamten Rotwildgebietes Bayerischer Wald dar. Im Jagdjahr 2002/03 lag der relative Rotwildabschuss für das gesamte Rotwildgebiet bei ca. 0,53 Stück / 100 ha – im Nationalpark leicht darunter mit 0,44 Stück/ 100 ha (Bayerische Landesanstalt für Wald und Forstwirtschaft (Hrsg.) 2004, S.8f).

Die leitende Forschungsfrage will Vorgaben und Ziele für das Schalenwildmanagement ergründen, aber abgesehen von subjektiven Artikeln in Zeitschriften oder den Interviewaussagen gibt es bis zur ersten Fassung der Nationalparkverordnung 1992 keinerlei Verbindlichkeiten. Der Bezug auf die im Nationalparkplan von 1995 formulierten Ziele ist eigentlich irreführend, weil es diesen Plan nur im Entwurf gegeben hat – er war nie behördlich festgesetzt. Erst der aktuelle Nationalparkplan von 2011 hat das Festsetzungsverfahren durchlaufen und kann als interne Zielvorgabe angesehen werden. Inwieweit die Ziele in welchem Zeitraum jedoch zu Standards werden sollen und ob es eine Evaluierung bezüglich einer Zielerreichung geben wird, ist unbekannt. Außerdem sind die Formulierungen sehr allgemein gehalten und es besteht ein großer Handlungsspielraum.

Zu beobachten war bei der Analyse der Entwicklung des Managements ein Wandel der Perspektive: Stand in der Anfangszeit noch der ‘naturnahe‘ Wald und dessen gesicherte Naturverjüngung im Fokus, so könnte man die moderne Ausrichtung als weniger polarisierend, vielmehr ausgleichend zwischen den Wildtieren und ihrem Lebensraum beschreiben. In der vorrangigen Zielsetzung ‘Erhalt der heimischen Wildarten‘ spiegelt sich diese Balance wider.

Ausblick

Gemäß dem Prozessschutzgedanken ist das übergeordnete Ziel für die Zukunft, aktive menschliche Eingriffe in die natürlichen Prozesse im Nationalpark weiter zu reduzieren. „Das Schalenwildmanagement in Nationalparken muß sich zunächst der Frage stellen, inwieweit eine Selbstregulation zugelassen werden kann und was dabei auf dem Spiel steht“ (Wotschikowsky 1981, S.100). Für die Nationalparkverwaltung gibt es hier noch große Spielräume, die Managementaktivitäten, wie Abschuss und Kirrung auf der Nationalparkfläche zu beenden und die Eingriffe zur Bestandeskontrolle auf die Wintergatter- und Saufänge zu konzentrieren. Zukunftsmusik aus Sicht des Nationalparks ist ein Umgang mit den

Rothirschen, der mit der Grundphilosophie besser zu vereinbaren ist als der Status quo. „Das Rotwild ist die Leitart, die für die meisten Diskussionen gesorgt hat und sorgt“ (J2). Nachdem das Projekt Rotwild auf neuen Wegen auf breite Ablehnung gestoßen ist, wird man auf diesem Feld in den nächsten Jahren wohl nur geringe Fortschritte erzielen können. Voraussetzung hierfür sind im Wesentlichen drei Aspekte. Zum Ersten ist das die Begleitung, Dokumentation und Evaluierung durch die Forschung. Dabei spielen Monitoringverfahren eine Schlüsselrolle; die Wechselwirkungen zwischen Vegetation bzw. Waldentwicklung, großen Pflanzenfressern und Prädatoren zu untersuchen, um gegebenenfalls auf bestimmte Entwicklungen reagieren zu können. Betont werden muss auch die Zusammenarbeit mit dem Nationalpark Šumava: ein grenzüberschreitendes Wildtiermonitoring sollte Grundlage für einen gemeinsamen Informationsstand sowie für einen einheitlichen Umgang mit den Wildtieren sein. Zweitens und die vielleicht noch wichtigere Voraussetzung ist die Akzeptanz der Menschen. Im Sinne des sog. ‘ecosystem approach‘, des ‘ökosystemaren Ansatzes’ soll die lokale Bevölkerung eingebunden werden (Heurich et al. 2009, S.145f). Dieser Ansatz steht für die Integration von sozialen, ökonomischen und umweltrelevanten Informationen über Ökosysteme. Er ist langfristig ausgerichtet und beachtet Ökosystemprozesse im Kleinen wie auch im größeren Rahmen von Landschaften. „Der Bevölkerung ist der Gedanke, dass man ein großes Gebiet weitgehend der Natur überlässt, noch viel zu wenig unter die Haut gedrungen […]; Wildnis gehört nicht in die Denkwelt der Menschen von heute“ (J4). Und drittens wird wohl erst die Rückkehr der Wölfe, den Entscheidungsdruck verursachen, der notwendig ist die Wintergatterproblematik noch einmal auf die Tagesordnung zu stellen.

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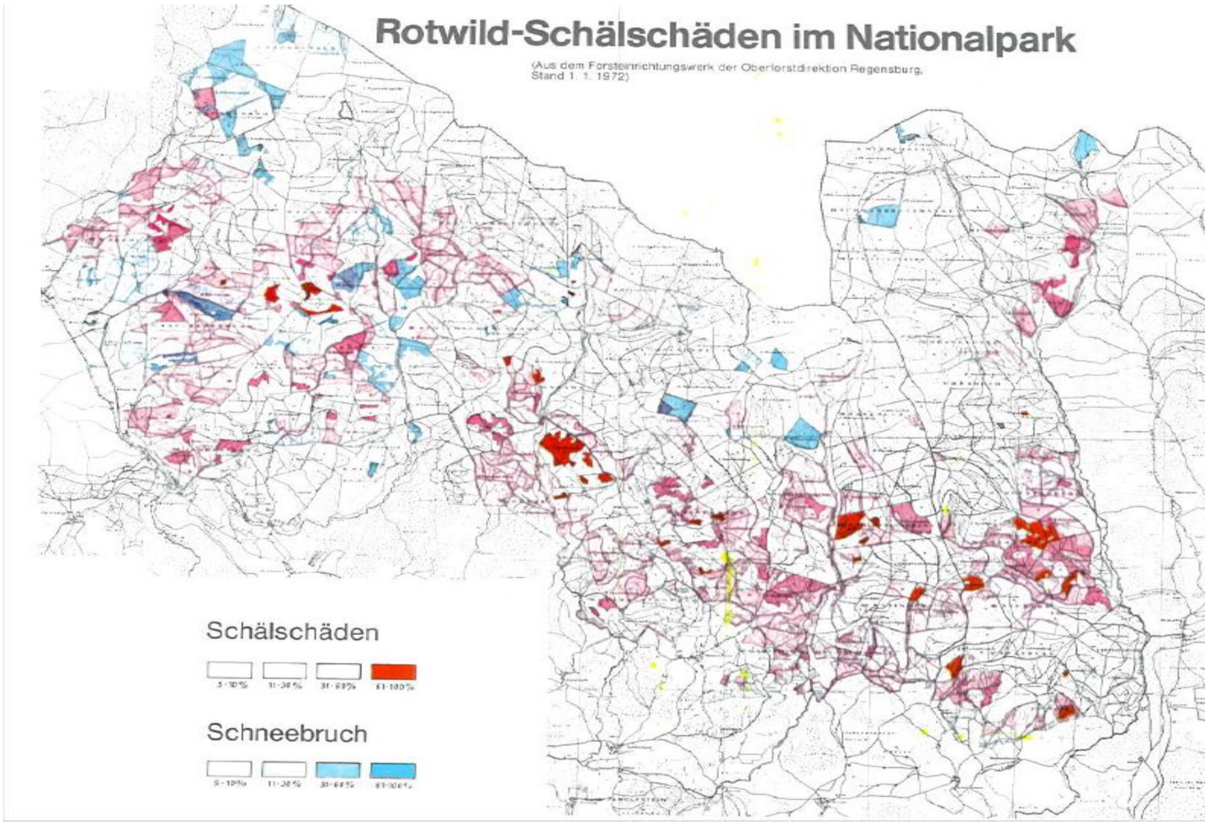
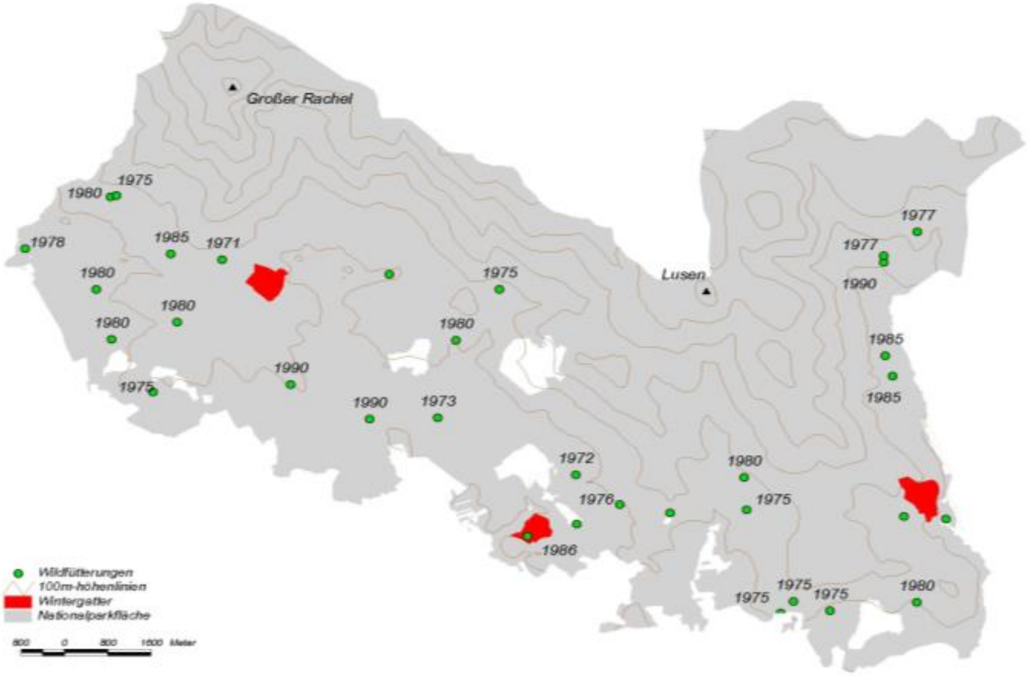
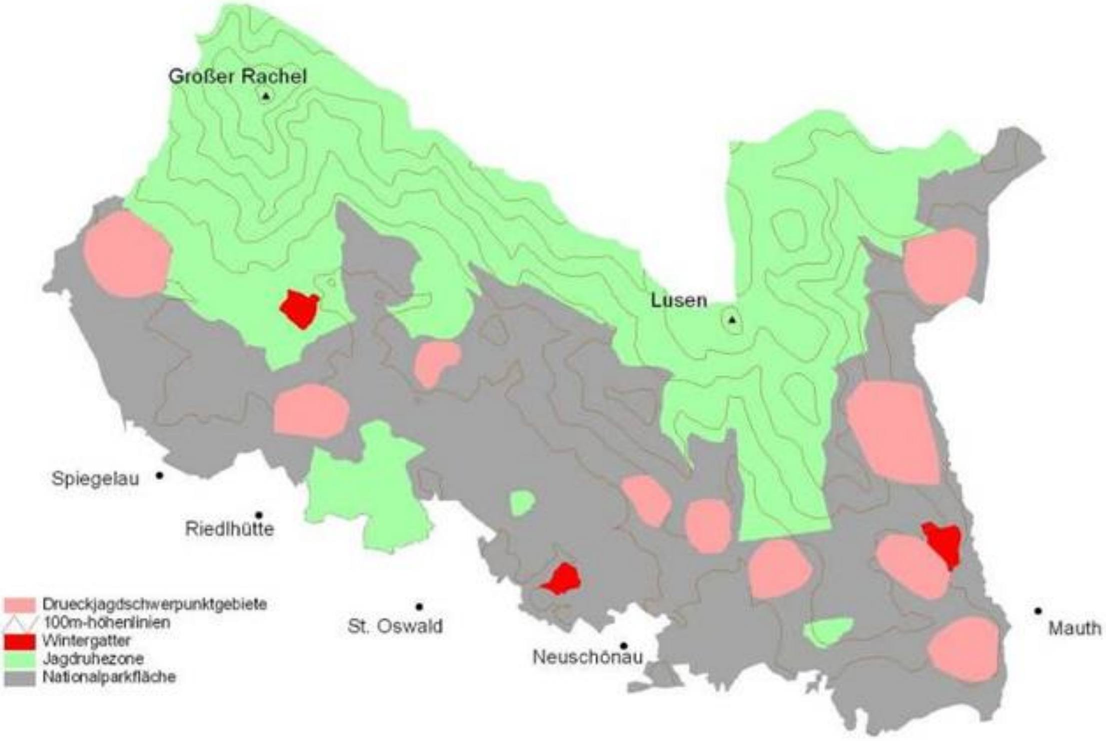
Abbildungen



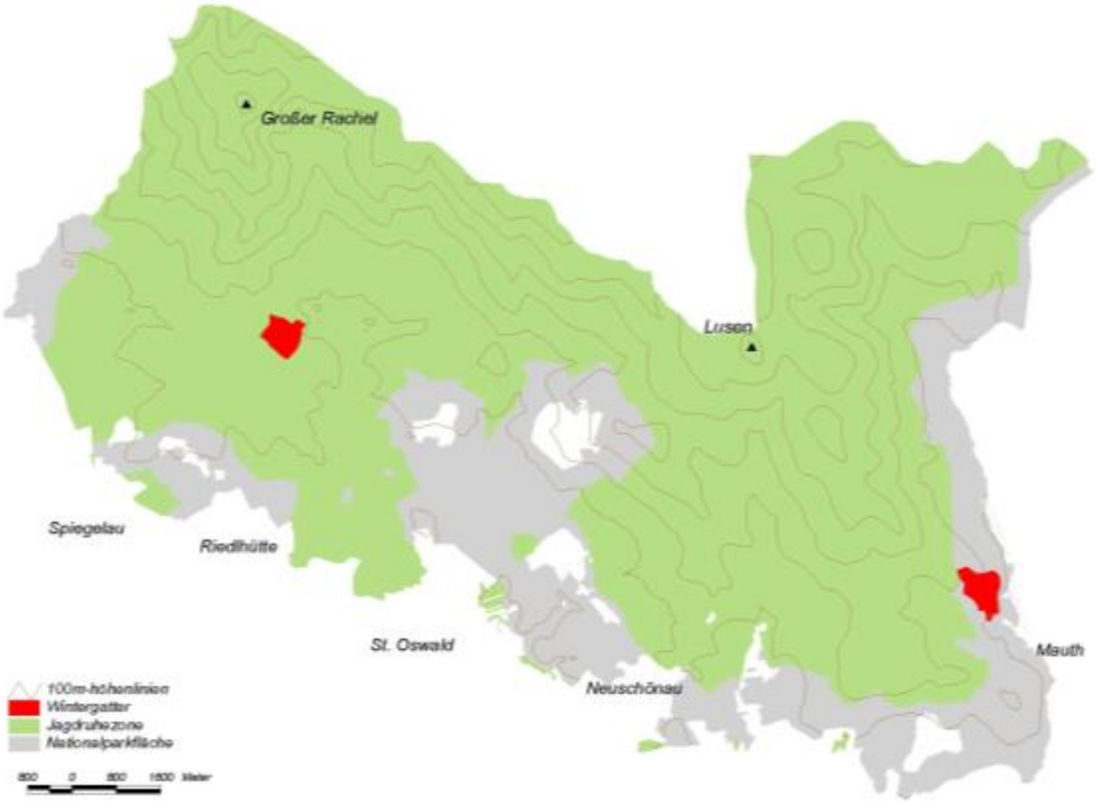
Karte 1: Verteilung der Rotwild-Schälschäden im Nationalpark aus dem Forsteinrichtungswerk der Oberforstdirektion Regensburg, Stand 01.01.1972
- Wotschikowsky 1981, S.27



Karte 2: Reh- und Rotwildfütterungen im Rachel-Lusen-Gebiet und Zeitpunkt ihrer Auflösung.



Karte 3: Huftiermanagement im Nationalpark Bayerischer Wald zwischen 1986 und 1997.



Karte 4: Huftiermanagement im Nationalpark Bayerischer Wald zwischen 1997 und 2012.

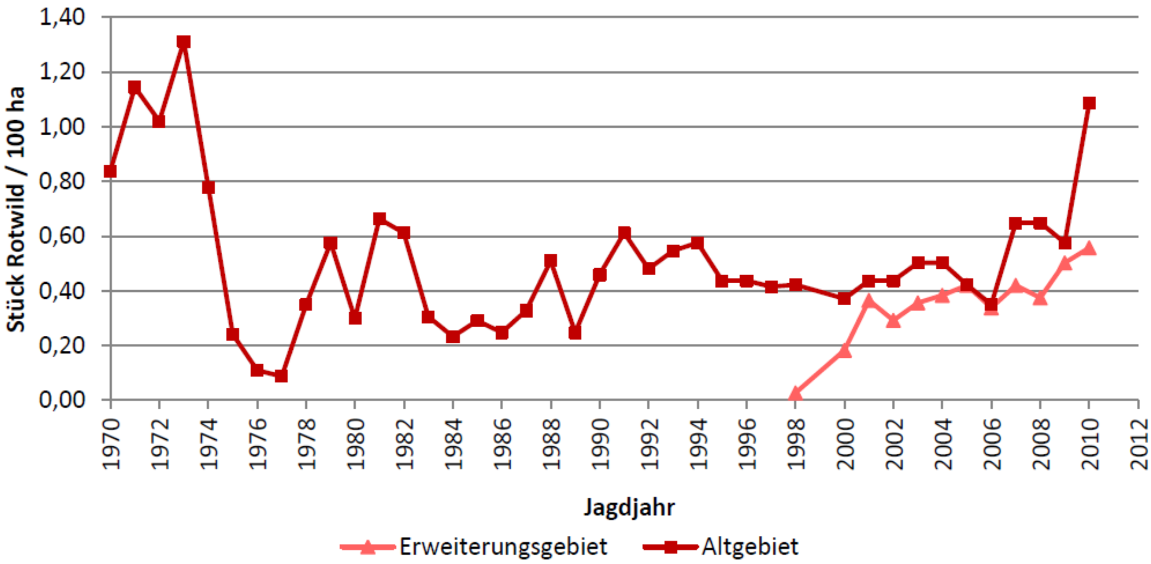


Abb. 1: Entwicklung der Abschusszahlen beim Rotwild (relativ pro 100 ha) von 1970 – 2010 (inkl. Fallwild)

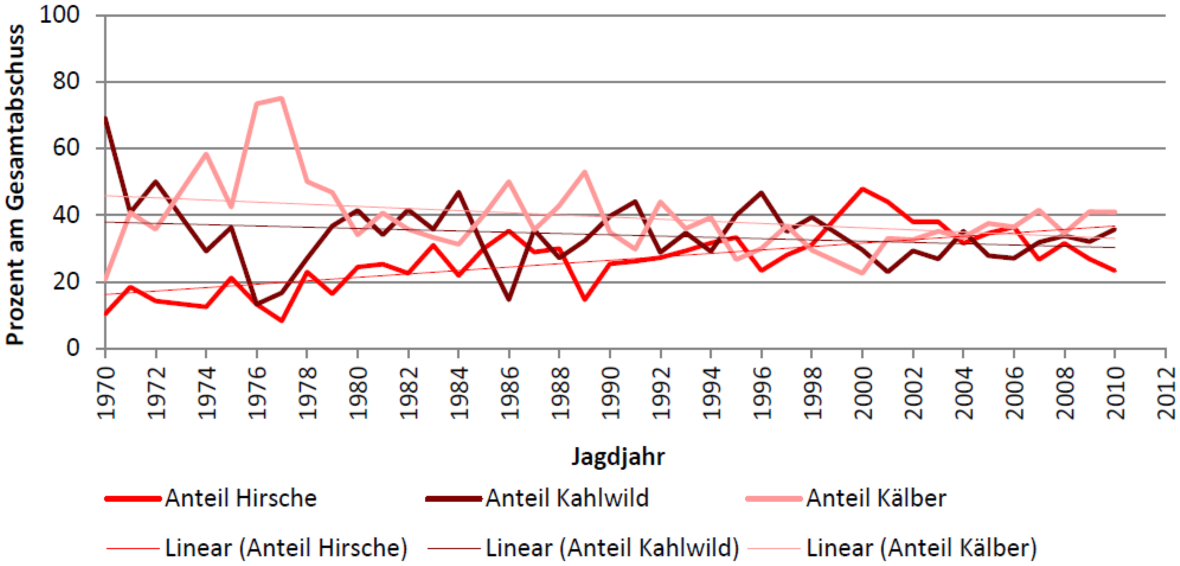


Abb. 2: Entwicklung der Anteile von Hirschen, Kahlwild und Kälbern am Gesamtabschuss Rotwild von 1970 – 2010 (inkl. Fallwild)

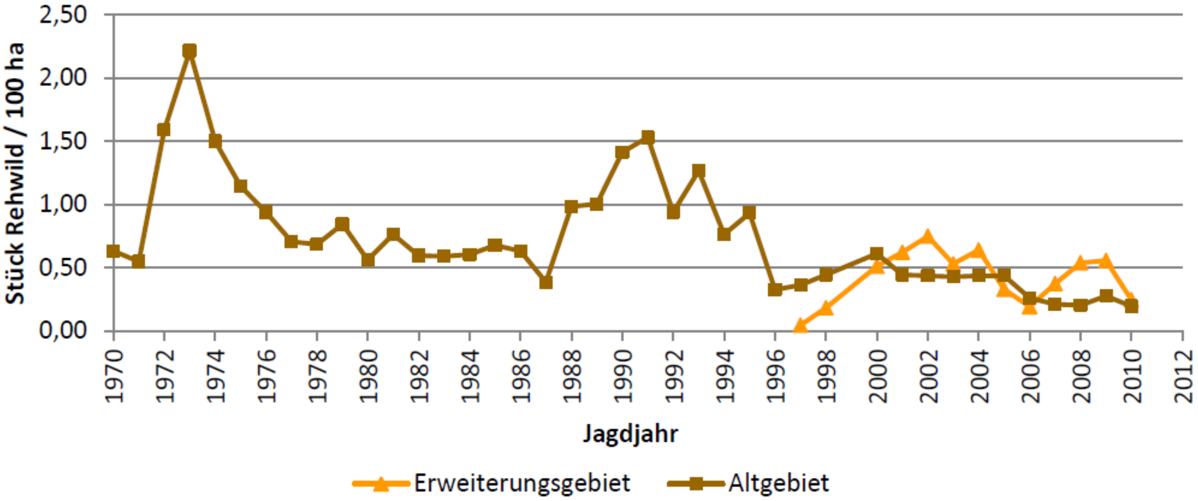


Abb. 3: Entwicklung der Abschusszahlen beim Rehwild (relativ pro 100 ha) von 1970 – 2010 (inkl. Fallwild)

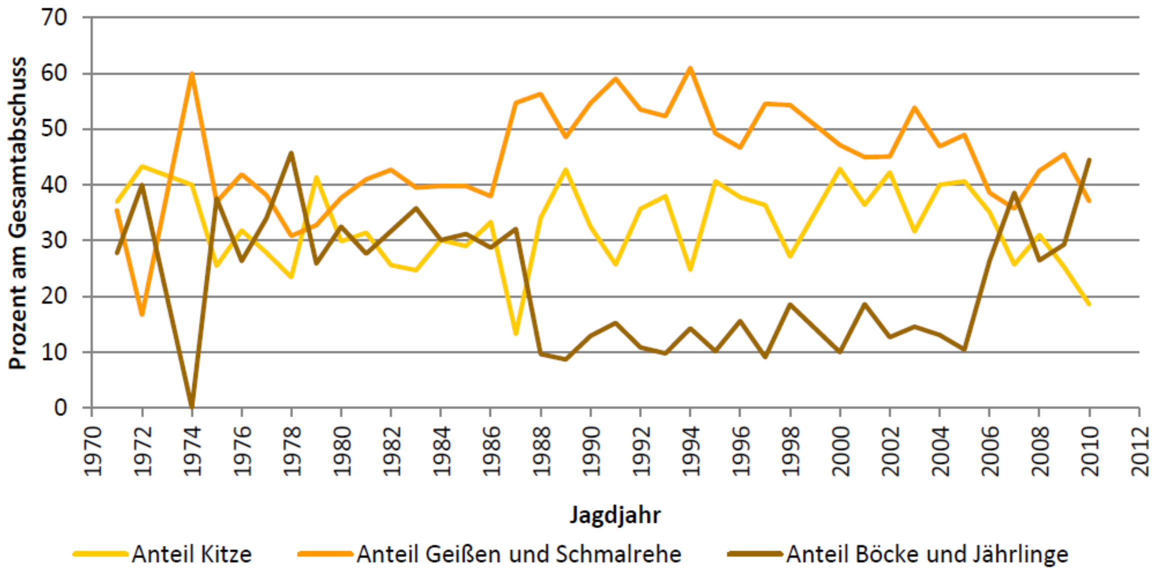


Abb. 4: Entwicklung der Anteile von Böcken, Geißen und Kitzen am Gesamtabschuss Rehwild von 1970 – 2010 (inkl. Fallwild)

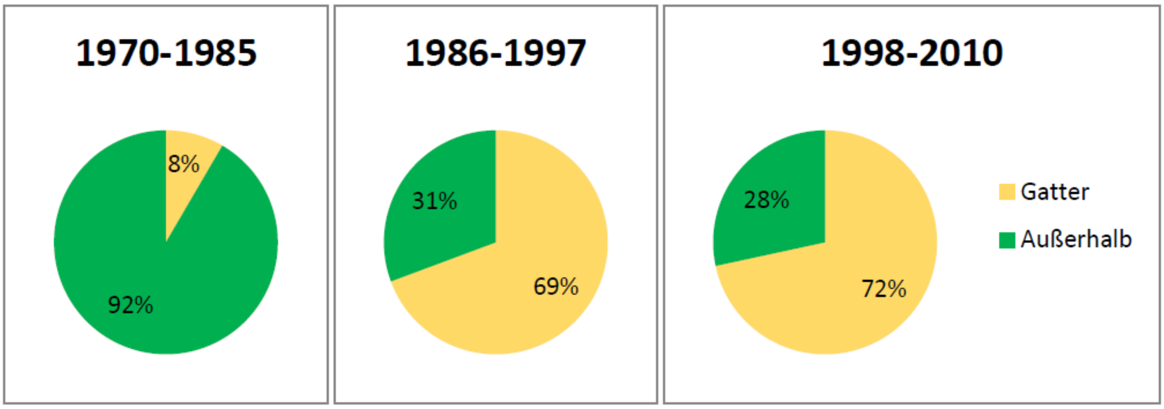


Abb. 5: Periodische Darstellung des Verhältnisses Gatterabschusses zu Abschuss außerhalb im Altgebiet

Anlage 2:

How to manage ungulates in a national park

Unintended side effects of management measures on the distribution of browsing pressure in the landscape

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Abstract

Most forests worldwide are intensively managed. The management of strictly protected areas, such as national parks, has to balance the protection of natural assemblages and processes with recreation and research. Wildlife management in European national parks has to deal with increased ungulate populations and their lack of predators. Management decisions require that management effects be disentangled from effects of space and physical environment. Here we measured the browsing activity of ungulates on 5,800 inventory plots in a montane forest national park. We tested the hypothesis that browsing in the landscape is mostly influenced by environmental variables not related to management of the national park. Our spatial additive logistic regression models for white fir, common rowan and European beech revealed a browsing intensity that allows regrowth of the tree species most palatable for ungulates. A comparison of different predictor sets revealed that management activities and space are most important in explaining the variation in browsing level. These quantitative results underline that management activities are of major relevance in the variation of browsing intensity, which strongly contrasts the aims of the national park to reduce anthropogenic influence on natural processes. Our results indicated that some of the management activities in the Bavarian Forest National Park are counterproductive for the conservation of natural processes, especially the establishment and positioning of winter enclosures, intervention zones and hiking trails throughout the park area. We therefore urge all park managers to carefully reconsider the necessity and effect of their management activities on the park aims.

Introduction

Large herbivores are vectors of important processes that significantly influence the structure, composition and development of ecosystems. Therefore, the management of large faunal elements in a landscape not only is decisive in assuring the completeness of the respective biocenosis but also has a considerable effect on the ecosystem itself [1-7].

The impact of deer browsing on forest ecosystems has attracted the interest of both foresters and conservationists during the last decades because the abundance of deer has increased rapidly owing to protection from human persecution, the lack of natural predators and the change of land-use practices [8-10]. Numerous studies have shown that ungulate browsing has a profound impact on forest ecosystems [1, 11-14]. Deer, as selective browsers or grazers, affect the growth and survival of many herb, shrub, and tree species and modify patterns of relative abundance and vegetation dynamics. Furthermore, over-browsing in forests reduces plant cover and diversity, which can change the successional pathways in forest ecosystems with consequences for the diversity of insects, mammals and birds and changes in nutrient and carbon cycling [3, 9, 15-17].

Most of recent studies have focused on the negative influence of ungulate browsing on the density and species composition of regenerated trees in commercial forests. The aim of management is to optimize opportunities for hunters while minimizing complaints of farmers and foresters [18]. The findings of these studies have been transferred to protected area management [19, 20]. But within protected areas, such as national parks, management objectives are different. According to the definition of the International Union for the Conservation of Nature (IUCN), protection of ecological processes (=natural process management), is — in addition to species protection, education and recreation — one of the most important management objective of national parks [21]. These designated goals of national parks require that human manipulation of the populations of large herbivores should be reduced to a minimum so that the natural dynamics of the system have more room to unfold [22]. But the species composition of national parks is often incomplete. For example, top predators or large herbivores are often lacking, and the areas are too small to comprise the entire processes they want to protect [23]. As a consequence, only some of the processes can be influenced by park managers, such as control measures, park zonation and position of hiking trails. Other processes cannot be directly addressed, such as land use and hunting outside the protected area. Therefore, park authorities often have to intervene to compensate for unfavourable framing conditions [18, 22, 24-26].

One important intervention tool is the control of herbivores. Examples are the culling of elephants in African national parks [27] and deer control in Central European and North American National Parks to compensate the absence of large predators, such as wolf, lynx and bear [28-30]. Through deer control, authorities try to prevent unnatural browsing pressure with its unintended effects on vegetation composition [31] and damages caused by deer in adjacent privately owned forests and fields [32]. But these control measures could profoundly influence natural processes that ultimately determine forest development, and even if the herbivore population is limited to a natural density, the influence of hunting could result in undesired side effects caused by antipredator behaviour of the ungulates [33]. The animals will try to avoid encounters with their predators, i.e. human hunters, by modifying their time–space behaviour [34]. Management measures other than direct control also could influence browsing. For example, winter feeding or the location of intervention zones can influence space use of the animals [35]. Also high touristic pressure via park roads and hiking trails might affect the distribution of browsing pressure, especially if the deer population is controlled and the animals therefore show a general fear of humans [36, 37].

The distribution of browsing pressure is influenced by abiotic and biotic environmental factors. On the landscape scale, topography is an important factor that determines the distribution of herbivores. Altitude, slope and aspect are the major characteristics that influence meteorological parameters, such as radiation, temperature, precipitation and snow height [38-41]. The structure of the forest stand, a biotic parameter, could influence the chance of a tree sapling being browsed because the structure greatly influences two important habitat variables, food and cover, which determine ungulate distribution [42-45]. The composition and structure of the regenerated trees themselves also plays an important role in the browsing risk. The palatability, nutrient content and taste of different plant species, but also their height, density and distribution affect their browsing risk [46, 47]. Also the physical and chemical characteristics of surrounding vegetation determine the risk of being browsed [48, 49]. According to [49], plants should be more at risk of being browsed among less-palatable or short neighbouring vegetation or when neighbouring vegetation is lacking. This is mainly because neighbouring vegetation is a potential alternative food resource and provides cover for tree saplings [50].

Here, we examine the influence of biotic and abiotic environmental and management-related factors on the distribution of browsing pressure in forest regeneration. We measured lead shoot browsing of common rowan (*Sorbus aucuparia)*, white fir (*Abies alba)* and European beech (*Fagus silvatica)* on 5,800 systematically distributed sample plots in the Bavarian Forest National Park. Our aims were to judge whether the strategy of the park administration to allow natural processes with as little interference as possible is achieved and to test the hypothesis that the distribution of browsing in the landscape is mostly influenced by environmental factors.

Study Area and Design

Natural Conditions

The Bavarian Forest National Park covers an area of 244 km² in south-eastern Germany along the border with the Czech Republic (49°3'19"N, 13°12'9"E). Together with the adjacent Bohemian Forest, the area comprises one of the largest contiguous forested areas in central Europe. The park was accredited by the International Union for Conservation of Nature (IUCN) in 1978 as category II.

The area is mountainous, with elevation varying between 600 and 1,453 m a.s.l. Mean annual temperature varies between 6.5 °C in the valleys and 3 °C along the ridges and at higher elevations. Mean annual precipitation varies between 830 and 2,230 mm, a considerable amount of which occurs as snowfall. Snow cover persists for seven to eight months at higher elevations and for five to six months in valleys.

Three major forest types are found within the national park. Above 1,100 m (16 % of the area), sub-alpine spruce forests with Norway spruce (*Picea abies*) and some common rowan prevail. On the slopes, between 600 and 1,100 m a.s.l. (68% of the area), mixed montane forests with Norway spruce, white fir, European beech and sycamore maple (*Acer pseudoplatanus*) occur. In wet depressions at the bottom of valleys (16% of the area), often associated with cold air pockets, spruce forests with Norway spruce, mountain ash and birch (*Betula pendula*, *Betula pubescens*) predominate. Since the mid-17th century, the area of the current national park was managed as a state forest, which led to a dramatic change in tree species composition. White fir originally accounted for at least 30% of the mixed mountain forests and decreased to the current <3% [51]. In the mid- 1990s, spruce trees of the national park were massively attacked by the spruce bark beetle (*Ips typographus*). By 2006, this resulted in the death of mature spruce stands over an area amounting to 6,000 ha [52, 53].

Park and Wildlife Management

One of the principles of wildlife management in the national park is the avoidance of control measures of the wild ungulate population through human intervention. However, because of the lack of natural predators and the additional aim of protecting privately owned forests and private property bordering the national park from damages, red deer and roe deer are controlled by hunting. To keep disturbances to a minimum, these measures have been spatially limited to a deer control area. This management zone comprises approximately 33% of the study area and serves as a buffer zone in the transition from the core zone to the landscape surrounding the national park.

The control quota considered the browsing level of preferred tree species to compensate for the dramatic decrease in white fir in the last centuries [54]. Browsing was surveyed every three years. The red deer density was estimated from coordinated counting’s during the winter and was allowed to vary between 100 and 300 animals. In 2002, 309 red deer were counted, and during the 2001/2002 hunting season, 81 were shot. The roe deer density was estimated by game wardens to be 500 to 750 animals in 2002, and 100 roe deer were shot during the 2001/2002 hunting season [25].

The range of red deer outside the park is restricted by law. The animals are no longer allowed to migrate to their natural winter habitat because these areas are outside the designated red deer range. Therefore, in the 1970s, the national park managers constructed four winter enclosures encompassing a 50–60 ha fenced area with a central feeding place. After the rutting period in October when the first snow falls, the red deer move to enclosures. Animals arriving later are trapped small pre-enclosures (less than 1 ha), and this entire group is then either led to the main enclosures for the winter or culled. Eighty percent of shot red deer are killed in this way. In the beginning of May after the flush of ground vegetation, the enclosures are opened. The purposes of this management measure are to compensate for the restricted winter habitat, to simulate the winter absence of the species in the montane forest and to control the population [55, 56].

One of the management objectives of the national park is tourism and recreation. For the >750,000 annual visitors [57], a network of 70 km of public roads (2.2 m/ha) and 351 km of marked hiking trails (14.5 m/ha) have been set up within the park.

Browsing Survey

A browsing survey was part of the 2002 forest inventory in the national park. During this inventory, 5,841 permanent inventory plots distributed in a 200 × 200 m grid were sampled. At each intersection, the forest regeneration was recorded on 25 m^2 circular inventory plots. Within this forest inventory, browsing of terminal shoots was measured [52]. Consequently, the response variable is the binary browsing damage (the tree is either browsed or not). The absolute number of common rowan, white fir and European beech and Norway spruce trees and the absolute number of browsed trees of each species were recorded (Table 1).

[Table 1 about here.]

Since we were interested in the contribution of abiotic and biotic factors, management activities and space in explaining the browsing distribution throughout the national park, we defined six groups of variables for space, management, topography, forest regeneration, forest stand and ground vegetation and recorded these for each inventory plot (Table 2).

.[Table 2 about here.]

The variable space, position of the inventory plot, was identified via spatial coordinates, including latitude and longitude.

The group of variables for management included the distance (m) from deer control areas, distance from hiking paths, distance from streets and distance from winter enclosures.

The group of variables for topography included altitude (m), hillside slope (degrees) and aspect (north or south orientation; binary variable).

The group of variables for forest regeneration included sapling height (cm) and sapling density measured as the number of trees per hectare <200 cm in height (log transformed). This threshold value guarantees consideration of trees easily reachable by only roe deer and red deer.

The group of variables for forest stand included the distance from the edge of the forest stand (m) and the categorical variables forest development phase, clear-cut, and type. The forest development phase specifies whether the plot is open, rich in structure, poor in structure, or a dead-wood plot. The covariable type classifies the plot as being part of either a subalpine spruce forest, a mixed montane forest or a valley bottom spruce forest, and the binary variable clear-cut indicates whether the plot is part of a clear-cut area or not.

The group of variables for ground vegetation is described as the percentage coverage of grass, fern, berry shrubs, raspberries/blackberries and moss. The amount of coverage is given in seven percentage classes (0: <0.1%; 1: 0.1–5%; 2: 6–10%; 3: 11–25%; 4: 26–50%; 5: 51–75%; 6: 76–100%). Because these intervals do not have consistent lengths, mid-scores were used to account for the differences. These mid-scores preserve the ordinal scale of the respective covariables.

Statistical Analysis

The probability of browsing damage for common rowan, white fir and European beech was modelled separately for each of the three tree species by means of a spatial additive logistic regression model, a special case of a generalized additive model (GAM) [58, 59]. The model relates the probability of a tree to have browsing damage to a function of the covariables discussed above via logit- transformation. In addition, each plot in the survey area is allowed to contribute to this function in a spatially smooth way to model spatial autocorrelation and unexplained heterogeneity. The numeric covariates sapling height, sapling density, altitude, hillside slope, and the five distance measures were assumed to have a smooth and nonlinear influence and were modelled by penalized cubic splines. Categorical variables and the mid-scored ordinal covariables describing ground cover were included linearly in the model. The longitude and latitude of the survey plots contributed to the model via bivariate thin-plate smoothing splines. The full model equation, including reference categories for the categorical variables, is given under (1).

We were especially interested in the contribution of certain groups of variables to the full model fit to assess their explanatory power for the browsing damage. Therefore, we summarize below the covariates of the full model, resulting in the six groups of variables given in Table 2. The variable group "remainder" contains all variables that do not fit in any of the other groups and is not of any further interest. When these groups of variables are used, the full model equation can be written more succinctly:

(1)

$$\mathbb{P}\,(\text{Browsing damage} \mid \text{Patch, Sapling height, Type}) =$$

$$s(\text{Latitude,longitude}) + f_{FR}(\text{Forest regeneration}) + f_{GV}(\text{Ground vegetation}) + f_{M}(\text{Management}) + f_{FS}(\text{Forest stand}) + f_{T}\,(\text{Topography}) + f_{R}(\text{Remainder}),$$

where the function s represents a smooth surface accounting for spatial autocorrelation and unexplained heterogeneity. The smooth functions $\tilde{f}_{FR}$, $\tilde{f}_{GV}$, $\tilde{f}_{M}$, $\tilde{f}_{FS}$, f_{T} and $\tilde{f}_{R}$ describe the functional form of the particular group of variables. For example, the function $\tilde{f}_{T}$ is defined as the additive combination of the variables describing topography (compare Table 2).

(2)

$$\tilde{f}_{T}(\text{Topography}) = \tilde{f}_{3}(\text{Altitude}) + \tilde{f}_{4}(\text{Hillside slope}) + \beta_{10}\text{Aspect},$$

with smooth functions f_3; f_4 and regression coefficient β_{10} as given in the full model equation (3). We fit the full model based on the model equation given in model equation (3).

(3)

Linear terms are given by β coefficients, nonlinear terms are given by functions $f_1, \ldots,$ f9, and s denotes a bivariate nonlinear term:

$\mathbb{P}$(Browsing damage | Patch, Sapling height, Type) =
$\text{logit}^{-1}(\beta_0 + \beta_1$Dominance wet areas + β_2Dominance bare soil + β_3Dominance bare
rock + β_4Dominance water + β_5Dominance grass + β_6Dominance fern +
β_7Dominance blueberry shrubs + β_8Dominance raspberries/blackberries +
β_9Dominance moss + β_{10}Aspect + β_{11}Boundary +
β_{12}(Forest development phase/rich - Forest development phase/open) +
β_{13}(Forest development phase/poor - Forest development phase/open) +
β_{14}(Forest development phase/dead - Forest development phase/open) +
β_{15}Cleared dead wood +
β_{16}(Type/Valley bottom spruce forests - Type/Mixed montane forests) +
β_{17}(Type/Subalpine spruce forests - Type/Mixed montane forests) +
f_1 (Sapling height) + f_2(log(Sapling density)) + f_3(Altitude) +
f_4(Hillside slope) + f_5(Distance edge of forest stand) + f_6(Distance winter enclosure) +
f_7(Distance deer control area) + f_8(Distance road) + f_9(Distance hiking path) +
s(Longitude, latitude-Coordinates Patch).

To assess the contribution of the groups of variables to the model fit, we used a graphical approach. More precisely, we considered box plots of the fitted linear predictors of the full model and the six groups of variables given in Table 2. The fitted linear predictors describe the log-odds for a browsed tree given the particular group of variables. If the box plot of the fitted values of a submodel show high variation, this corresponds to a high contribution of the associated variables to the full model fit. For details on estimation and inference in generalized additive models, we refer the reader to [60]. All computations were performed in R [61], version 2.13.2, using the add-on package mgcv [62] for fitting GAMs.

Results

Our analysis of the data collected in the 2002 forest inventory indicated that 0.3% of the Norway spruce trees, 6% of European beech trees, 11% of white fir trees, and 32% common rowan trees were browsed (Table 1).

Common Rowan Browsing Model

The models for common rowan browsing were based on 4,738 trees located on 1,261 plots throughout the Bavarian Forest National Park (Table 1). As described above, we were interested in the contribution of certain groups of variables to the full model fit. Therefore, we fitted the full model including all covariates and investigated the variance of the fitted values of groups of variables only for space, management, topography, forest regeneration, forest stand and ground vegetation.

[Figure 1 about here.]

Box plots of the fitted linear predictors of the particular groups of variables (Figure 1) can be interpreted as the log-odds for a browsed common rowan tree given the respective variables. Therefore, all values above the grey zero line represent observations with an increased chance of browsing, whereas values below the grey zero line represent observations with a decreased chance of browsing. Not surprisingly, the fitted values based on the full model showed the most variation. Besides the spatial term, the covariates for management activities in the national park explained a considerable amount of the full model fit as the corresponding box plots showed higher variations. The box plots of topography, forest regeneration, forest stand and ground vegetation showed less variation and thus contributed less to the full model fit.

White Fir Browsing Model

The models for white fir browsing models are were based on the 2,498 trees located on 651 plots throughout the Bavarian Forest National Park (Table 1).

[Figure 2 about here.]

The importance of our six submodels for describing the browsing damage on white fir can be seen in the corresponding box plots (Figure 2). The fitted values based on the full model were the most variable. The box plots of the fitted values for space and management showed more variation than those for topography, forest regeneration, forest stand and ground vegetation. Therefore, the spatial term and management variables contribute most to the full model fit. These interpretations correspond to the results gained for the model for common rowan browsing.

European Beech Browsing Model

In the forest inventory of 2002 in the Bavarian Forest National Park, the damage status of 32,461 European beeches was recorded (Table 1). As this huge amount of data cannot be handled by the gam function, we used only part of the data for the analysis. We sampled 16,365 beech trees from the full data set, and considered the location of the trees to account for the influence of the geographical distribution of the trees throughout the study area.

[Figure 3 about here.]

The box plots were similar to those found for the models for common rowan and white fir browsing (Figure 3). Again, the fitted values based on the full model were the most variable. In this case, the box plot for the management variables showed the most variation, followed by the box plot of the spatial submodel. Thus, these variables explain most of the full model fit. The topography and the forest regeneration submodel showed similar variations and hence make a comparable contribution to the full model fit. In contrast, fewer variations for the forest stand and ground vegetation submodel were observed. Thus, the results of all three browsing models were consistent in that the management variables and the spatial term contribute highly to the full model fit. Moreover, the variables for ground vegetation and forest stand were of minor importance in all browsing models.

Discussion

Abundant deer herds can have major impacts on the integrity of protected areas negatively. These conflicts could possibly be reduced by limiting the numbers of deer herds through hunting or control measures [19, 20]. However, such attempts to limit ungulate densities often lead only to a reduced browsing level on spruce and other non-palatable tree species but not on deciduous trees [20]. In the Bavarian Forest National Park, with its benign-neglect strategy of the past 40 years, ungulate densities are limited by culling the herd in the winter enclosures, driving hunts and hunting from high seats [25] .

Our analysis of tree browsing data collected in the 2002 forest inventory indicated that ungulates browsed mostly on the preferred common rowan (32% of the trees), followed by white fir (11%) and European beech (6%), with only little browsing of the less palatable Norway spruce (0.3%) (Table 1). Although the browsing pressure on common rowan was highest, it can be considered comparatively low considering its attractiveness to herbivores [63, 64]. These 2002 levels were lower than those observed in the 1992 forest inventory, namely 2% of the Norway spruce trees, 10% of the European beech trees, 25% of the white fir trees and 38% of the common rowan trees [52]. These results document that the wildlife management activities of the Bavarian Forest National Park instated after 40 years were effective in limiting browsing to a relatively low level. This overall browsing level is low enough for the regenerated trees to survive and grow beyond browsing height [65, 66]. Especially for white fir, whose proportion of the forest composition has been reduced in the last centuries from >30% to currently 3% in the study area [51], the management objective of securing its regeneration was reached. Therefore, additional or management tools, such as protecting single trees or fencing, are no longer necessary.

According to [67, 68], the ungulate density is the most important factor determining the browsing pressure. Other factors, such as forest structure and ground vegetation, seem to be important only at low to medium deer densities [49, 69]. Because of the relatively low browsing pressure revealed in our study, it is justified to take a closer look at other factors determining the distribution of browsing pressure in the landscape. The main result of our study was that management-related factors showed by far the highest contribution to the model fit. This was true for all examined tree species. Also the spatial position of the sample plot was of importance, mainly because the spatial component accounted for spatial autocorrelation and unobserved heterogeneity. Hence, this variable captured amongst others the influence of all spatially structured effects that we did not take into consideration. All other factors played only a minor role. These results are surprising because we expected that environmental factors would be highly important for the distribution of browsing pressure.

The low influence of topography on the chance of a tree species being browsed could be due to the lack of great variations in slope and aspect in the national park, unlike the variations in an alpine terrain [52]. A greater variability in topography would possibly influence the animal's habitat choice more, such that south- and west-facing slopes would be preferred in winter. A seasonal migration of deer in the study area from ridges to valleys should lead to a higher browsing pressure in the valleys. But since most of the red deer are kept in enclosures in winter, the valleys are not reached. Therefore, management in the national park blurs the effect of elevation, which might be high in a natural system.

Also the effect of ground coverage of herbaceous plants was unexpectedly low. [49, 70] and observed that ungulates forage in forest gaps rather than in closed forests. This was explained by the better light conditions in gaps formed by the opening of the forest canopy, which leads to a domination of herbaceous vegetation, which in turn serves as food for red deer and roe deer [71, 72]. Also clear-cut areas deliver a high habitat quality for deer because of the nutrient-rich understory vegetation, which has led to an observed high browsing pressure in other studies, especially when the surrounding forests are less-structured monocultures [43, 73, 74]. If valuable food resources are abundantly available, the impact of herbivores on tree regeneration might be not as strong [75]. For example, when the abundance of raspberry and blackberry plants increase, the browsing pressure on tree saplings decreases [76, 77] . A similar effect of grasses, a preferred food resource of red deer, would be expected [72, 78]. In the Bavarian Forest National Park, the forest habitat changed drastically because of an intense bark beetle (*Ips typographus*) infestation that affected 3,700 ha of dominant spruce stands [79]. This bark beetle kills mature Norway spruce trees, which results in an increase in both the quantity and quality of biomass available for consumption by herbivores. The ensuing canopy openings are distributed throughout the area and therefore have an impact on most of the deer inhabiting the area. As a consequence, the influence of herbaceous ground cover and forest structure at the plot level might be negligible because it is influenced strongly by nearby canopy openings caused by bark beetles. This might explain why forest structure, which has been found to have an impact on browsing probability in other studies [43, 80-82] had only a minor impact in our study.

Of all environmental parameters tested, the structure of the regeneration had the highest impact on browsing probability, especially the height and density of regenerated trees. Previous studies have reported that trees suffering the highest browsing pressure are those at ungulate shoulder height [13, 48]. A higher sapling density provides potential forage, but if the sapling density exceeds a certain threshold, large ungulates might face difficulties in moving, which leads to a reduced browsing probability [12, 80].

Our results revealed the importance of national park management for the distribution of browsing pressure. Wildlife control affects browsing not only through the direct limitation of animal populations, but also through a change in animal behaviour. Deer avoid future encounters with humans by increasing alertness [83] or by changing their habitat choice [36]. In our study, this behavioural change would be reflected in the variable distance to deer control areas, i.e. the farther the distance to the control area, the higher is the browsing pressure. By avoiding control areas, deer seek to reduce their risk of being killed. Because deer are not able to differentiate between hunters and humans in general, hunting can also lead to chronic stress [84]. Therefore, deer try to avoid not only hunters but also tourists, which mean that areas used by humans, e.g. public roads and hiking paths, are an important factor determining the distribution of deer [37, 43]. Our results showed that these effects lead to changing browsing patterns and therefore might extensively influence the ecological system [33, 34].

Winter enclosures are a management tool to reduce browsing impact in winter by luring the animals to feeding stations enclosed with a fence. This management measure is used to prevent browsing outside the enclosure and leads to a high browsing impact within. After the first animals have migrated into the enclosure, the gates are closed. Animals that appear later are caught and fed in a pre-enclosure and are then either culled or led into the main enclosure. Consequently, the animals roam for a long period in the vicinity of the enclosure before they are trapped, which leads to a higher browsing pressure near the winter enclosures. Therefore, as expected, in our study, the browsing level decreased with increasing distance to the enclosure. [85] found extensive browsing damage in the proximity of open feeding stations. But the browsing pressure around open feeding stations should be higher than that around winter enclosures that fence in the majority of the animals. Therefore, on the one hand winter enclosure as a management tool reduces the size of the deer herd if animals in the pre-enclosure are culled and has a positive influence on forest development, but on the other hand they lead to a higher browsing pressure in the vicinity of these structures.

Conclusions

Our study showed that even if it is possible to mimic the influence of natural predators in limiting ungulate densities to an extent that allows native tree species to regenerate successfully, the management measures used might influence the distribution of the browsing pressure to a greater extent than abiotic and biotic environmental factors. The unintended influence on the distribution of browsing pressure will lead to a “landscape of fear” not caused by natural predators but rather by park management. This influence might also have a long-term influence on further forest development by changing successional pathways.

To reduce these unintended effects, we recommend shifting the control measures from the deer control area to the hunting grounds adjacent to the national park. It would be also important to remove the winter enclosures or at least feeding in the pre-enclosure should be stopped after the hunting season and the trail system at least should not be enhanced, but if possible reduced. Also the recolonization of wolves in the area should be considered as these natural predators would guarantee a more natural time–space behaviour of the ungulates, but such an action would have to be accepted by the people inhabiting the park surroundings.

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Tables

Table 1: Distribution of browsing damage on four tree species. The numbers correspond to the absolute number of trees.

Tree common name	Number of unbrowsed trees	Number of browsed trees	Total number of trees
Common rowan	3,588	1,150	4,738
White fir	2,252	246	2,498
European beech	15,452	913	16,365
Norway spruce	62,189	2,006	60,183
Sum	22,114	2,558	24,672

Table 2: Variables within the major groups of variables

Variable group	Variables in the group
Spatial	Latitude, longitude
Management	Distance to deer control area, distance to hiking trails, distance to streets, distance to winter enclosure
Topography	Altitude, slope, aspect
Forest regeneration	Sapling height, log(sapling density)
Forest stand	Distance to edge of forest stand, forest development phase, forest type, clear-cut
Ground vegetation	Dominance of grasses, ferns, berry shrubs, mosses, berry shrubs

Figures

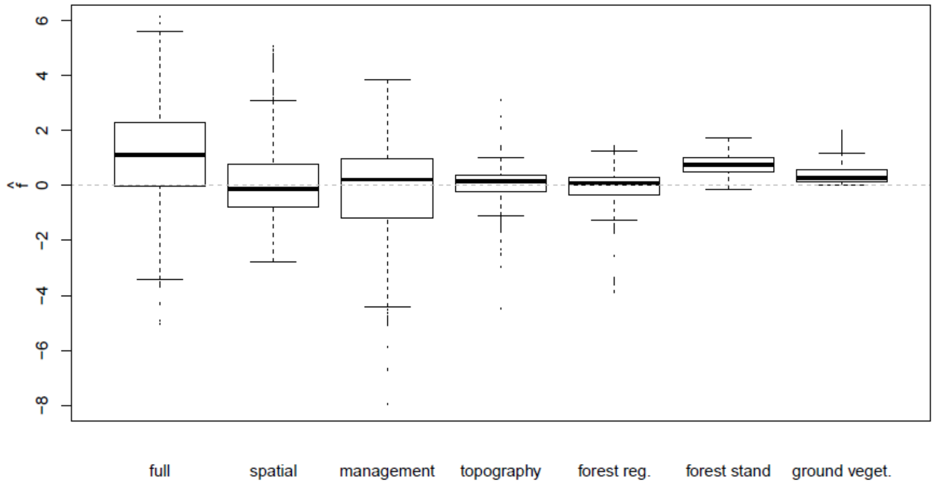

Figure 1: Common rowan browsing model. Box plot of the fitted linear predictors based on the full model and the models containing only variable space, management, topography, forest regeneration, forest stand or ground vegetation.

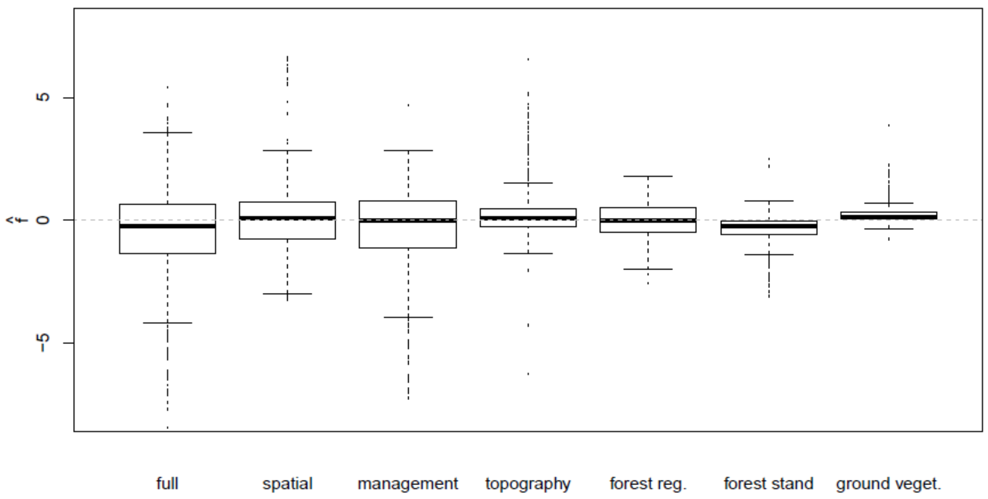

Figure 2: White fir browsing model. Box plot of the fitted linear predictors based on the full model and the models containing only the variable space, management, topography, forest regeneration, forest stand or ground vegetation.

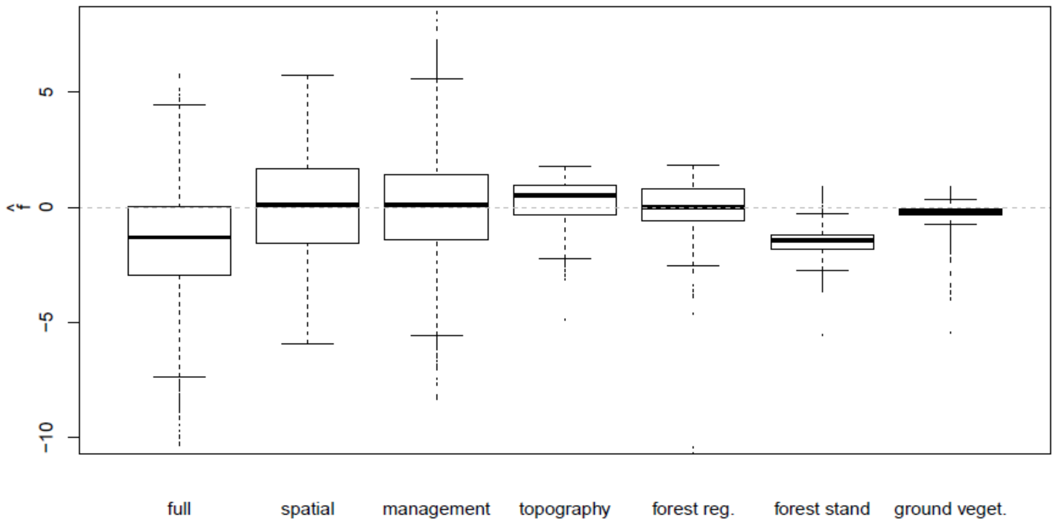

Figure 3: European beech browsing model. Box plots of the fitted linear predictors based on the full model and the models containing only the variable space, management, topography, forest regeneration, forest stand or ground vegetation.

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Anlage 3:

Title: What determines home range size? The importance of a landscape's spatial configuration

Running Head:

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Abstract

Most animals restrain their movement activities to familiar areas. What factors shape the dynamics of such home ranges remains largely unclear. However, understanding home range establishment and shifts is highly relevant for basic science and conservation. Evidently home ranges are influenced by the underlying landscape. Only recently landscape composition, i.e. the fraction of different land cover types, has been shown to affect home range size. So far, studies dealing with variation in home range size do not take into account the explicit spatial configuration of the landscape, a factor which is known to be of central importance for (meta-)population dynamics. We here quantify the effect of landscape configuration on home range sizes across multiple spatio–temporal scales using GPS data from red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in the National Park Bavarian Forest, Germany. We show that the spatial configuration of the landscape is the most important factor explaining home range size. Furthermore, we find that as these species differ in habitat requirements the correlation between home range size and landscape configuration depends on a species' life history: while roe deer increase their home range size with increasing landscape patchiness, the relationship is unimodal for red deer. Our results are robust at all tested spatio–temporal scales.

Keywords: animal movement, spatial ecology, telemetry, spatial heterogeneity, patch, landscape structure, space use, landscape configuration

Introduction

With increasing human wildlife conflicts it is necessary to know the status and predict the changes of wildlife behaviour in general and specifically of animal movement patterns (Wilcove and Wikelski 2008). This information is especially needed for animals which live in landscapes that are subject to changes, either due to anthropogenic land use like agriculture or to natural changes such as fires and epidemics. Moreover, a correct interpretation of the causes of animal movement and dispersal is pivotal for understanding habitat selection and more generally the diversity and distribution of species (e.g. Chave et al. 2002).

Most animals do not move randomly through a landscape (Nathan et al. 2008, Fronhofer et al. 2012) and seem to restrain their movement activities to familiar areas. While central place foragers, such as bees or ants, return to their nest after a foraging bout and territorial animals, such as felids, defend well defined landscape stretches, a large majority of animals use familiar areas without defending them. This last behaviour leads to the establishment of home ranges, which are generally defined as the spatial expression of all behaviours an animal performs in order to survive and reproduce (Burt 1943). As home ranges link individual movement paths to dispersal and (meta-)population dynamics understanding why and how home range sizes vary between and among species is a fundamental issue in ecology.

While theory still struggles to explain the emergence of home ranges (Börger et al. 2008) the availability of large movement data sets allows us to formulate some sensible hypotheses. Due to progress in GPS–sensor technology and satellite techniques we are nowadays able to track animals over long time spans with high temporal and spatial resolution and to analyse their habitat requirements and movement paths (Tomkiewicz et al. 2010). Such analyses have shown that home range sizes may e.g. depend on body size (Swihart et al. 1988), forage availability (Tufto et al. 1996) or intra- (Riley and Dood 1984, Saïd et al. 2005) and interspecific competition (Loft et al. 1993).

Besides these factors it is well known that the spatial arrangement of different habitat types can influence the distribution of large mammals (Clutton-Brock and Harvey 1978, Kie et al. 2002). Animals need to find resources, usually defined as food, but are also relying on resources like e.g. shelter against predators. One single habitat patch may not always satisfy all needs at the same time. Typically forage–rich habitats providing high quality food are more exposed, while closed habitats provide cover resulting in a trade–off in habitat choice (Hebblewhite et al. 2008, Godvik et al. 2009, Bjø-rneraas et al. 2011). Today a large number of studies have shown that the landscape is an essential determinant of home range size and dynamics in general. These studies usually only take the dominant habitat type within a home range into account, i.e. the landscape composition is included only as the fraction of e.g. meadow or forest within the home range and usullay only the dominant habitat type is considered (Frair et al. 2005, Börger et al. 2006b, Rivrud et al. 2010). Yet, the explicit spatial configuration of habitat patches, the arrangement of all land cover types within the home range, and the size of these patches is not taken into account.

A natural landscape is heterogeneous in respect to resources, as these are often autocorrelated and form resource clusters or patches of varying size and density (see figure 1). An artificial landscape (figure 1 B), derived from our true natural landscape, that keeps the fraction of land cover types constants but orders them randomly in space illustrates that changing a landscapes spatial configuration will affect home range size. In such a randomized landscape home ranges would become much smaller, as a large number of different land cover types can be found on a much smaller scale. On the other hand, an artificially ordered landscape (figure 1 C) would lead to longer movement paths, e.g. when an animal needs to reach the land cover type ”meadow” after having been in ”deciduous forest”, for example, and therefore needs to cross a block of ”mixed forest”.

As the explicit spatial configuration of land cover types will determine the movement path of an animal searching for food or shelter we hypothesize that the spatial configuration is a central determinant of home range size. Therefore, we here analyse the effects of landscape configuration, the spatial arrangement of the habitat patches within a home range, on the variation in home range size at several spatio–temporal scales with two sympatric species, red and roe deer. Considering multiple spatial and temporal scales when defining a home range is important as mechanisms that affect variation in home range size may differ depending on the scale under investigation (van Beest et al. 2011).

[Figure 1 about here.]

Our analysis is the first to show that the spatial configuration of the landscape is the most important factor explaining home range size at all tested spatio–temporal scales for both red and roe deer. Generally, smaller home ranges can be found in more patchy landscapes due to shorter paths between different land cover types. Furthermore, we find that the correlation between home range size and landscape configuration depends on a species' life history.

Roe deer shows a linear relationship with the landscape configuration and establishes larger home ranges in more aggregated landscapes. Red deer on the other hand reveals a humped shaped relationship between home range size and landscape configuration and has the largest home ranges at intermediate aggregated landscapes. The two species differ in habitat requirements and red deer are able to utilize specific large patches more efficiently which leads to smaller home range in high aggregated landscapes when these patches occur.

Material and Methods

Study area and deer data

The study was conducted in the National Park Bavarian Forest which covers ca. 240 km^2 and is situated in southeastern Germany. The area is mountainous, with three major forest types: sub–alpine spruce forests, mixed montane forests and spruce forest in the valley bottom. Since the mid–1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*).

From 2002–2010 red and roe deer were caught and marked with GPS collars (Vectronic Aerospace, Berlin, Germany). The most common sampling design was to mark deer in late winter and retrieve the collars after a year by collar drop–off or recapturing, allowing to use the same collars on new individuals. Home ranges were estimated from 65,669 GPS location points collected on 32 collared red deer (14 males, 18 females) from 2002–2009 and from 29,672 GPS location points collected on 40 collared roe deer (24 males, 16 females) from 2005–2010.

Please find a more detailed description of the study area, data collection and processing in Appendix A.

Home range estimation

Home ranges were estimated with the most common approach, the fixed kernel method (Worton 1989, Calenge 2006) using the reference method for the smoothing factor h (Kernohan et al. 2001). We used three different home range isopleths (90 %, 70 %, 50 %) as spatial scale to test conservative kernels and to prevent artefacts. In addition, all home ranges were estimated on three temporal scales: monthly, biweekly and weekly. We only estimated home ranges for individuals with at least six relocations for the temporal scale under study (month, biweek, week). We checked for plausibility of the data (Börger et al. 2006b) and calculated home ranges only if they had at least 95 % overlap with the land cover map.

Land cover types and environmental data

To characterise the landscape in our study area we considered five land cover types: coniferous forest, deciduous forest, mixed forest, meadow and regeneration areas (bark beetle areas). Anthropogenic areas and water bodies were not taken into account as they cover only a small area within the study area. The main land cover classification was derived through digitalization from aerial images from the year 2008. However to take account of the dynamic in the forest due to bark beetle outbreaks, we checked the land cover classification for every year to derive appropriate maps for every single year.

As a measure of the landscape's spatial configuration we calculated different landscape indices within a given home range (McGarigal et al. 2002). Here we quantify the landscape configuration as the percentage of like adjacencies (PLADJ) as this index could be shown to be most reliable (see Appendix B for details). In the following we will refer to this index as patch aggregation index.

In addition to the spatial configuration we also included standard environmental data into our analysis. Temperature and rainfall data were obtained from the Waldäuser weather station located within the study area in the National Park Bavarian Forest (940 m a.s.l., (48° 55′ 45″ N, 13° 27′ 50″ E). We used the deviations of temperature and rainfall from the yearly mean values for each temporal scale to account for the effect of climatic variability. Furthermore, we estimated the mean elevation of the home ranges using ASTER GDEM (resolution: 30 m; http://asterweb.jpl.nasa.gov/gdem.asp).

As these environmental variables are not the focus of this article they will not de discussed in detail below.

Statistical Methods

To investigate the influence of different land cover types, climate variables and the landscape configuration on home range sizes, we used linear mixed models on the log transformed home range areas (km^2), using the software R version 2.13.2 (R Development Core Team 2011) and the package "lmer" (Bates et al. 2011). For a detailed description of the statistical methods please see Appendix C.

We considered the patch aggregation index and the land cover types coniferous forest, deciduous forest and meadow as well as the environmental factors precipitation, temperature and elevation as fixed effects. We fitted random intercepts for each individual (ID), different sexes and the year the GPS–locations were sampled. We repeated the analysis for the three kernel isopleths and for the three temporal scales. Preliminary analysis showed that the variables elevation and landscape index have a humped shaped relationship with the home range size in the red deer data and we used here a quadratic fit for the approach. Full models with landscape index and without landscape index were compared with the AIC criterion.

Results

The role of landscape configuration

Home range sizes varied across all spatio–temporal scales, especially for red deer. The fixed effects of the most parsimonious models explained between 19 % and 24.53 % of the observed variation in home range size for red deer and between 4.19 % and 18.82 % for roe deer. The main random effect for both species was the variable ID, whereas roe deer showed additionally an effect of sex, hence all analysis for roe deer are split for the sexes. Our measure for landscape configuration, the patch aggregation index (PLADJ), showed for both species a high explanatory value. More specifically, all models with landscape configuration (patch aggregation index, PLADJ) showed significantly better results in explaining variation in home range sizes (figure 2 and Appendix F, Table 3). Our results show that by including the explicit spatial configuration of land cover patches the variation in home range size can be better explained as by including only fractions of dominant habitat type within a home range, as the patch aggregation index accounts additionally for patch arrangement and size.

[Figure 2 about here.]

Landscape configuration explains home range size

The patch aggregation index (PLADJ) showed a high explanatory value for the variation in home range size of both study species, red and roe deer. The relationship in red deer revealed a humped shape fit, leading to high home range sizes with intermediate patch aggregation, while roe deer continuously increased their home range size as patches become more aggregated (figure 3).

[Figure 3 about here.]

The pattern described above showed an increasing explanatory value at larger spatial scales. A trend in the pattern on the temporal scale was pronounced in 90 % kernels with highest explanatory value on the monthly scale, but less clear on the biweekly and weekly scale for the red deer data (see Appendix H).

Discussion

Most empirical studies on home range dynamics and size take into account vegetation, i.e. the fraction of land cover types, and climate but not the explicit spatial configuration of a landscape (Börger et al. 2006a, Rivrud et al. 2010, van Beest et al. 2011). The present study is, to our knowledge, the first to investigate the effect of a landscape's spatial configuration on variation in home range sizes on different spatio–temporal scales for two sympatric ungulate species, red and roe deer. We demonstrate that by including aspects of the landscape configuration, here patch aggregation, predictions of home range size can be significantly improved. All models including spatial configuration were significantly superior to models that only included the fraction of land over types (figure 2). This result is not fundamentally surprising, as it becomes clear from the artificial ordered landscape in figure 1 C, when we consider an animal, which for example is located in the land cover type "deciduous forest" and needs to reach the land cover type "meadow" to gain food resources and hence needs to cross a large block of ”mixed forest” to reach its goal. While the same animal will reach its goal in a very patchy landscape (figure 1 B) with a much shorter movement path. True landscapes are a mixture of patches which differ in size and habitat type and an animal will establish an home range according to its needs within this landscape. Hence, the home range will contain resources patches to fulfill the needs and patches an animal is only traversing when it contains no value for the animal. While previously studies accounted for the land cover fraction within a landscape, for example by calculating the productivity of an landscape and here considering only the dominant habitat type of, e.g. meadows as food resource, the size of a home range will additionally be defined by the arrangement of the patches within the landscape, as we show here and this aspect is so far too often not accounted for.

The role of landscape configuration

Red and roe deer differ in their habitat requirements and behaviour: red deer are widely roaming animals and intermediate feeders and cosume both, high and poor–quality food (Hofmann 1989). In our study area very large patches are typically regeneration areas, i.e. land stretches that have suffered from massive bark beetle outbreaks during the 90s. These outbreaks affected an area of approximately 6000 ha especially in the subalpine regions, leading to sunny openings and large regeneration areas (Mueller and Fagan 2008, Heurich et al. 2010, Lausch et al. 2011). After a first succession phase the characteristics of these areas provide exceptionally good habitat for red deer, with abundant food and shelter at the same spot. Roe deer characteristically show smaller movement radii, are very selective feeders and only consume highly digestible forage (Barančeková et al. 2009) and are therefore highly dependend on the land cover type meadow.

When considering only the habitat requirements, for example food resources, we can also see an effect in home range size varation in our analysis, but only a small part can be explained. As shown in figure 3 smaller home ranges occur when the amount of valuable resources is a large part within the home range (regeneration areas for red deer, meadow for roe deer). When we add the explicit spatial configuration of our landscape the explained deviance is increasing. The consitency of the effect of the landscape configuration over all spatio–temporal scales shows its importance in deterining the size of a home range.

Our study shows that as patch aggregation increases home range size generally increases. This happens because typically animals have two contrasting needs, (1) to find forage resources and (2) to find shelter. These needs are typically connected to different habitats which may even change over time forcing an animal to move between different resource patches. In very fine grained landscapes different land cover types will co–occur at small spatial scales which means that movement paths will become shorter leading to small home ranges.

This effect is highly visible in our study (figure 3), and furthermore due to the differences in habitat preferences leads to different relationships for the two species. In roe deer both sexes show a linear relationship. In red deer the relationship is humped shaped due to patches which provide exceptionell good resources for red deer as they can fulfill two contrasting needs (food and shelter) and leads to the unimodality of home range size and patch aggregation.

Environmental parameters

Additional explanatory value was achieved through the variable elevation especially in red deer. Similar to the landscape index, elevation had an unimodal fit which is driven by the regeneration areas that are located at higher altitude. This underlines the important role of these areas in determining home range size. As pointed out above the occurrence of regeneration areas leads to very small home ranges as this habitat provides food and shelter at the same time. Rivrud et al.(2010) pointed out the importance of climatic variables on home range size. We could find some effects in roe deer, but the overall explained deviance was not large (please see Appendix F and Appendix G for further details).

Concluding remarks

Although home ranges have been studied extensively for quite some time, it is only recently that the importance of the underlying landscape has been recognized. An increasing number of studies could show that the fraction of different habitats present in a landscape at least partially explain home range size (Frair et al. 2005, Börger et al. 2006b, Rivrud et al. 2010). Yet, it is intuitively clear that more fundamentally the spatial configuration of land cover types should determine home range size too, as these external conditions define the actual distances animals have to cover in order to satisfy different needs. Nevertheless, this spatial aspect has, to our knowledge, not been emphasized so far in explaining variation in home range size. Here, we have shown that the spatial configuration of the landscape is the most important factor explaining home range size for two exemplary deer species. Our results were robust at all tested spatio–temporal scales.

Acknowledgements

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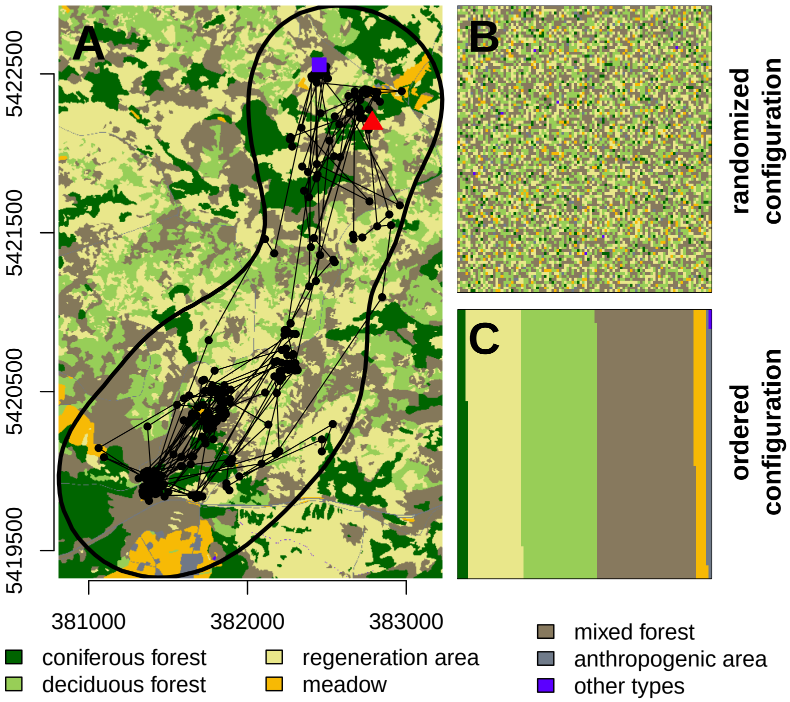
A
B
C
5422500
5421500
5420500
5419500
381000
382000
383000
randomized configuration
ordered configuration
coniferous forest
deciduous forest
regeneration area
meadow
mixed forest
anthropogenic area
other types

Figure 1

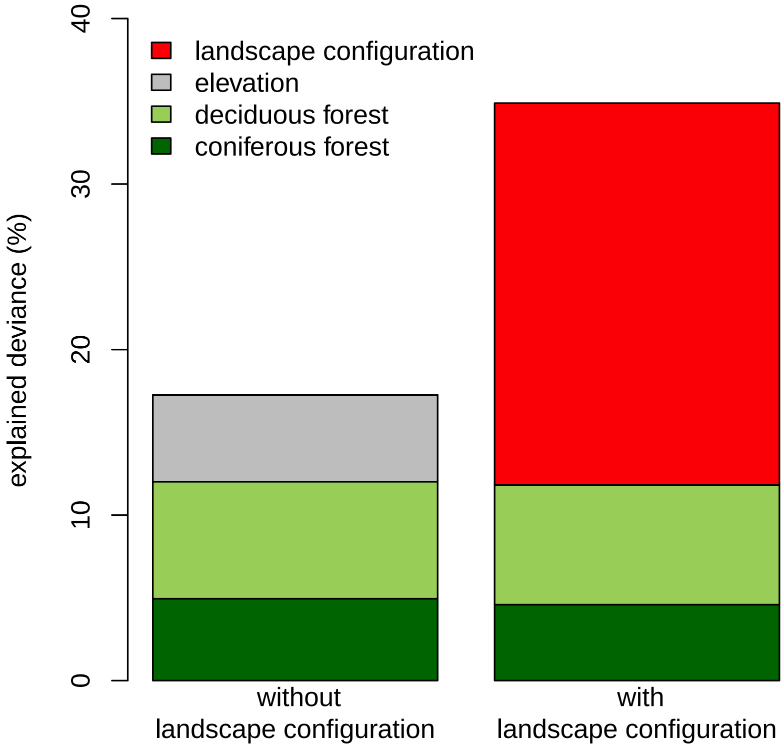
40
30
20
10
0
explained deviance (%)
landscape configuration
elevation
deciduous forest
coniferous forest
without
landscape configuration
with
landscape configuration

Figure 2

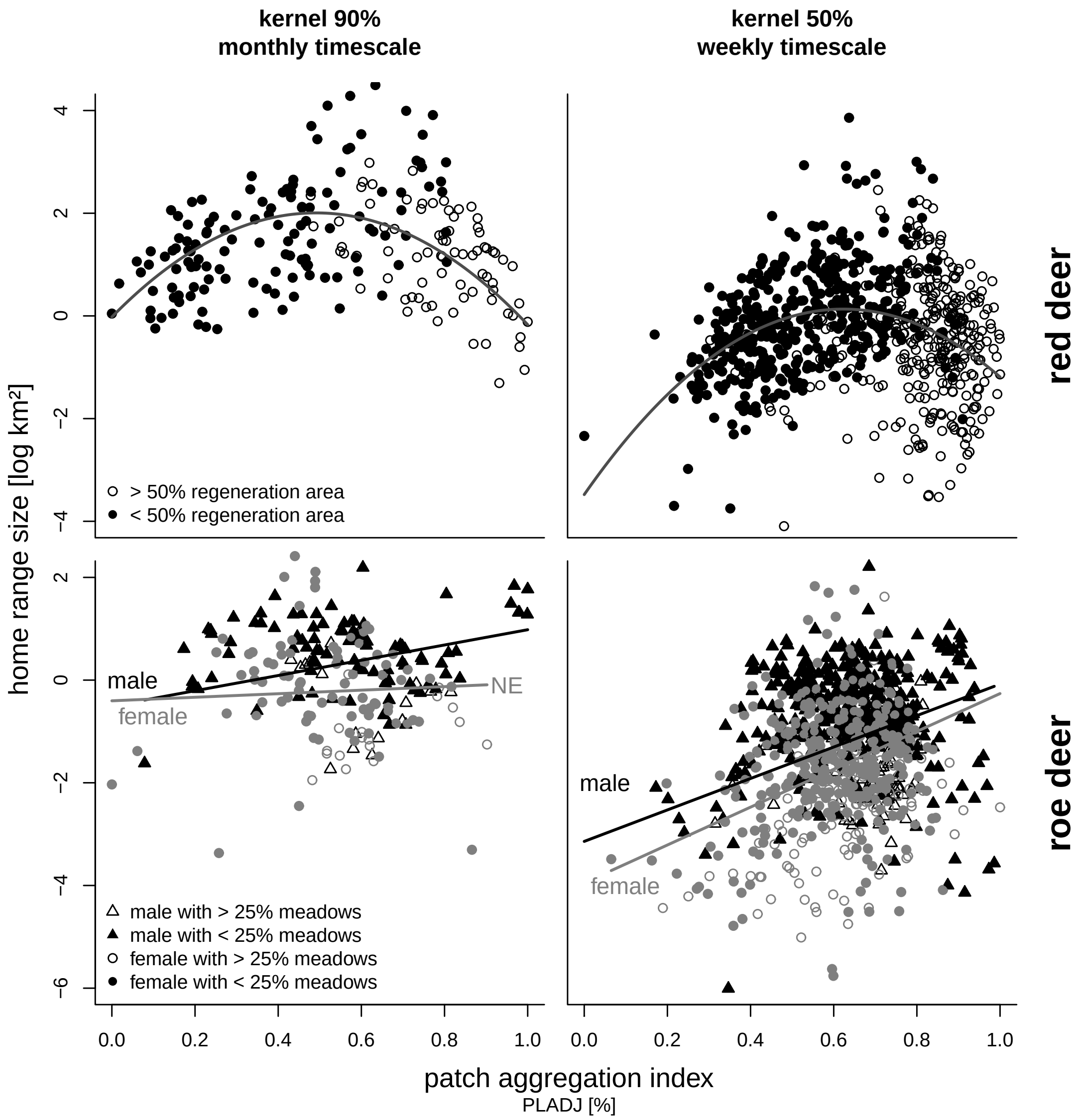
kernel 90%
monthly timescale
kernel 50%
weekly timescale
red deer
roe deer
home range size [log km²]
○ > 50% regeneration area
● < 50% regeneration area
male
female
NE
△ male with > 25% meadows
▲ male with < 25% meadows
○ female with > 25% meadows
● female with < 25% meadows
4
2
0
−2
−4
−6
0.0
0.2
0.4
0.6
0.8
1.0
patch aggregation index
PLADJ [%]

Figure 3

APPENDIX A:
Study area and deer data

Study area

The study was conducted in the National Park Bavarian Forest situated in southeastern Germany along the border to the Czech Republic ($49^\circ\,3'\,19''$ N, $13^\circ\,12'\,9''$ E). The National Park covers an area of 240 km^2. Adjacent to the park, on the Czech side of the border, lies the Šumava National Park with its 640 km^2. These protected areas are embedded within the Bavarian Forest Nature Park (3070 km^2) and the Šumava Landscape Protection Area (1000 km^2). In its entirety, the area is known as the Bohemian Forest Ecosystem. The area is mountainous, with a variation in elevation between 600 and 1450 m.a.s.l. The mean annual temperature varies between 3°C and 6.5°C along higher elevation and ridges. The mean annual precipitation is between 830 and 2230 mm. Within in the park, three major forest types exists: above 1100 m are sub–alpine spruce forests with Norway Spruce (*Picea abies* L.) and some Mountain Ash (*Sorbus aucuparia* L.), on the slopes, between 600 and 1100 m altitude, are mixed montane forests with Norway Spruce, White Fir (*Abies alba* MILL.), European Beech (*Fagus sylvatica* L.), and Sycamore Maple (*Acer pseudoplatanus* L.). In the valley bottoms, spruce forests with Norway Spruce, Mountain Ash, and birches (*Betula pendula* ROTH. and *Betula pubescens* EHRH.). Since the mid–1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2007, this had resulted in the death of mature spruce stands over an area amounting to 5,600 ha (Müller et al., 2008).

Deer data

From 2002–2009 red deer were caught during winter, after procedure approved by the national ethical board. Red deer were captured and marked with GPS collars (Vectronic Aerospace, Berlin, Germany) in box traps with side windows after they were lured in with food. Here no immobilization was necessary. A second approach was to tranquillize deer by dart gun on sides where they were attracted by food. We collared 32 deer (14 male, 18 female). Four individuals were collard two or more times over the single years. Roe deer were captured during the winter month (October to March) in the years 2005–2010 using wooden box traps. The animals were lured into the traps with pomace, maize or silage. The traps were set during the evening and inspected the following morning. A captured roe deer was grasped by the legs, pulled from the trap, and held firmly by its legs and GPS-collars were attached within 5 minutes. Therefore, it was not necessary to immobilize the animals. Animal handling was performed in compliance with German laws and regulations. A total of 40 roe deer (24 male, 16 female) were collard, with five animals collard two or more times over the single years. The most common sampling design was to mark roe and red deer in late winter and retrieve the collars after a year by collar drop–off or recapturing, allowing the collars to be used on new individuals. We removed spatial outliers (i.e. locations that are not located within 5 km around the Bohemian Forest) and we also removed all temporal false fixes (i.e. locations taken only a few seconds apart) in both data sets. This leads to a removal of 19 % of the raw data for red deer and 16 % for roe deer. We used only the summer months (May–October) for the analysis and classified the samples from the multiple collard animals over the single years as independent. We took a random sample for animals with sequences of short time intervals (e.g. location point taken every 15 min) to ensure that the locations have an interval of one hour. The elapsed time between locations for each animal averaged 157.57 min for red deer and 365.77 min for roe deer with an overall position acquisition rate of 72.8 % and an median accuracy of 16.5 m (Stache et al., 2012)

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APPENDIX B:
Area dependencies of landscape indices

Buffers around 90 % kernel home range centres (monthly scale, n=214) from the red deer data set were drawn from 500 m to 7000 m in 500 m steps.

We then calculated six landscape indices for each buffer circle (area–weighted mean patch area (AREA_AM), contagion (CONTAG), percentage of like adjacencies (PLADJ), landscape division index (DIVISION), effective mesh size (MESH), aggregation index (AI)). Afterwards we run a mixed model to check for size dependencies of the indices. In total 13.42 % of calculated buffers were excluded from further analyses as they contained more than 5 % missing values in land cover data.

The analysis of the area–dependency of the landscape indices revealed a high size–dependency of the metrics AREA_AM, DIVISION and MESH, hence these indices were excluded from further analyses. Additionally the indices CONTAG, PLADJ and AI were highly correlated with each other (Pearson's correlation Index > 0.8).

The PLADJ index accounts not only for patch size but also on patch shape (McGarigal et al., 2002), and furthermore shows the least dependency on area, so we choose this index for all further analysis. The indices AI and CONTAG show essentially the same results.

The software tools R version 2.13.2 (R Development Core Team, 2011), GRASS 6.4.1 (Grass Development Team, 2012) and FRAGSTATS v3 (McGarigal et al., 2002) were used for the analyses.

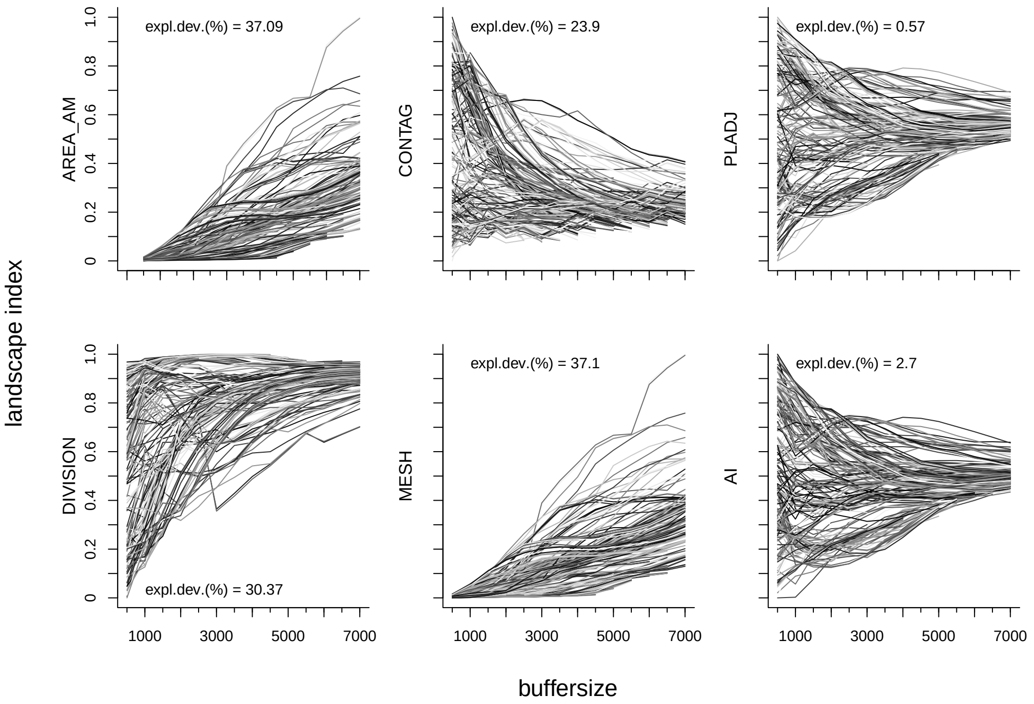


Figure 1: Overview of the size dependencies of six calculated landscape metrics analysed with a mixed model. Buffer index values belonging to the same home range centre point are connected with a line. The explanatory value (expl.dev(%)) of the size dependency for each landscape index is drawn within the plot.

Literature Cited

Grass Development Team, 2012. Geographic Resources Analysis Support System (GRASS) Software, Version 6.4.1. *http://grass.osgeo.org.*

McGarigal, K., S. Cushman, M. Neel, and E. Ene, 2002. FRAGSTATS v3: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. *http://www.r–project.org.*

APPENDIX C:
Statistical methods

Following the framework of Zuur et al.(2009) for mixed effect models, we first identified the best structure for the random effect term. We fitted random intercepts for each individual (ID), different sexes and the year the locations were sampled, using the full model with respect to fixed effects terms and using the REML criterion for fitting. We started with the full random term and then simplified the model. Afterwards we compared the models with an ANOVA and the best model was evaluated with the Akaike Information Criterion (AIC). For variable selection, models were fitted with a maximum likelihood criterion. We considered as fixed effects the land cover types coniferous forest, deciduous forest and meadows, as climate variables precipitation and temperature, and also took into account altitude and one landscape index. The final models where fitted using the REML criterion. We derived minimal adequate models by backward stepwise selection using a t–value of 2 as a threshold for inclusion (Tremblay and Ransijn, 2011).

Colinerarity between the variables was checked beforehand using Pearson's correlation (the threshold was set to 0.7, - 0.7 respectively) and highly correlated variables were excluded. This leads to a removal of the land cover types mixed (correlated with deciduous, regeneration and elevation) and regeneration (correlated with mixed and elevation).

To evaluate the importance of landscape configuration for the model fit, we compared the full models (random term and all fixed effects and additionally one model contained the landscape index as fixed effect whereas it was missing in the other model) with the AIC criterion (please see Appendix F for the results).

We repeated the analysing steps for the three definitions of home range size and for the three definitions of temporal scale.

The software tools R version 2.13.2 (R Development Core Team, 2011) using the packages "lmer" (Bates et al., 2011) and "LMERConvenienceFunctions" (Tremblay and Ransijn, 2011) were used for the analyses.

Literature Cited

Bates, D., M. Maechler, and B. Bolker, 2011. lme4: Linear mixed–effects models using S4 classes. *R package version 0.9.*

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. *http://www.r–project.org.*

Tremblay, A. and J. Ransijn, 2011. LMERConvenienceFunctions: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. *R package version 1.6.8.3.*

Zuur, A., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith, 2009. Mixed effects models and extensions in ecology with R. Springer, New York, United States.

APPENDIX D:

Home range size of red and roe deer across spatio–temporal scales

Summary statistics of male and female red (A) and roe deer (B) home range sizes (km^2) across spatio–temporal scales (N = Number of samples included in home range estimation).

Home ranges were estimated with the fixed kernel method using the reference method for the smoothing factor h (Worton, 1989; Kernohan et al., 2001). The software R version 2.13.2 using the package “adehabitatHR” was used for the analysis (R Development Core Team, 2011; Calenge, 2006).

A	**Red deer (*Cervus elaphus*) – males**			
		Kernelsize		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	Mean (range)	11.05 (0.58–89.62)	5.60 (0.32–37.47)	3.00 (0.17–20-91)
	N	93	94	95
biweekly				
	Mean (range)	7.73 (0.43–103.98)	4.15 (0.16–51.25)	2.28 (0.08–26.53)
	N	179	181	183
weekly				
	Mean (range)	6.75 (0.07–190.85)	3.51 (0.03–93.34)	1.91 (0.02–47.40)
	N	338	340	342

Continued on next page

	Red deer (*Cervus elaphus*) – females			
		Kernelsize		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	Mean (range)	4.14 (0.27–15.22)	2.04 (0.14–8.62)	1.11 (0.07–5.26)
	N	115	115	115
biweekly				
	Mean (range)	4.06 (0.07–32.81)	1.99 (0.04–13.33)	1.07 (0.02–7.00)
	N	221	221	221
weekly				
	Mean (range)	3.84 (0.07–67.08)	1.94 (0.04–34.90)	1.07 (0.02–18.81)
	N	411	411	411

B	**Roe deer (*Capreolus capreolus*) – males**			
		Kernelsize		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	Mean (range)	1.96 (0.18–8.94)	1.07 (0.05–4.30)	0.61 (0.03–2.17)
	N	108	111	112
biweekly				
	Mean (range)	1.99 (0.005–11.37)	1.10 (0.002–6.35)	0.64 (0.001–3.68)
	N	247	253	258
weekly				
	Mean (range)	2.10 (0.005–40.21)	1.16 (0.002–17.05)	0.67 (0.001–9.09)
	N	465	473	483

	Roe deer (*Capreolus capreolus*) – females			
		Kernelsize		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	Mean (range)	1.30 (0.03–11.19)	0.62 (0.01–4.11)	0.34 (0.01–2.24)
	N	97	99	99
biweekly				
	Mean (range)	1.15 (0.01–13.44)	0.58 (0.01–6.81)	0.32 (0.004–3.69)
	N	225	228	228
weekly				
	Mean (range)	1.04 (0.01–22.09)	0.56 (0.006–11.56)	0.32 (0.003–6.23)
	N	441	451	448

Literature Cited

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**:516–519.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh, 2001. Analysis of animal space use and movements. In J. J. Millspaugh and J. Marzluff, editors, *Radio Tracking and Animal Populations*, pages 126–164. Academic Press, San Diego, California, USA.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing *http://www.r–project.org.*

Worton, B., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**:164–168.

APPENDIX E:

Table of random effects for mixed models on all spatio–temporal scales for red and roe deer

Table of random effects and standard deviation (SD) of the linear mixed models for all spatio–temporal scales for both species, red (A) and roe deer (B), with roe deer split into sexes. The main random effect for both species was the variable ID, whereas roe deer showed additionally an effect of sex, hence all analyses for roe deer are split into the sexes. Within the analysis of the random structure the variable year the locations were sampled had no effect on the random structure in both species.

A	**Red deer (*Cervus elaphus*)**			
		Kernel size		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	random effect	0.34	0.32	0.32
	SD	0.58	0.56	0.56
biweekly				
	random effect	0.30	0.30	0.02
	SD	0.55	0.55	0.55
weekly				
	random effect	0.32	0.31	0.30
	SD	0.56	0.55	0.55

Continued on next page

B **Roe deer (*Capreolus capreolus*) – males**

Timescale		**Kernel size** **90 %**	**70 %**	**50 %**
monthly				
	random effect	0.35	0.34	0.28
	SD	0.59	0.60	0.53
biweekly				
	random effect	0.58	0.46	0.35
	SD	0.76	0.68	0.59
weekly				
	random effect	0.99	0.97	0.34
	SD	0.99	0.98	0.93

Roe deer (*Capreolus capreolus*) – females

Timescale		**Kernel size** **90 %**	**70 %**	**50 %**
monthly				
	random effect	0.67	0.52	0.46
	SD	0.82	0.72	0.68
biweekly				
	random effect	0.36	0.35	0.35
	SD	0.60	0.59	0.61
weekly				
	random effect	0.22	0.34	0.34
	SD	0.47	0.58	0.58

APPENDIX F:

Tables of explained deviances of the mixed models for red and roe deer and model comparison between mixed models with and without spatial configuration

In red deer only the two land cover types, namely coniferous forest and deciduous forest showed an effect on home range size. However there was no clear pattern and a positive relationship of coniferous forest and deciduous forest with home range size was only found in 90 % and 70 % kernel on the monthly scale and 90 % kernel on the weekly scale. In addition to land cover types the variable elevation showed a high amount of explanatory value on all scales with a quadratic relationship in respect to the home range sizes. The climatic variables precipitation and temperature did not influence red deer home range size at any spatio–temporal scale.

Table 1: F–values and explained deviance (%) are shown retained from the mixed model calculated for all temporal (monthly, biweekly and weekly) and all spatial scales (90 %, 70 % and 50 % isopleths) for red deer with ID as random structure. The variables elevation and PLADJ were fitted as quadratic terms.

Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
monthly					
	50	PLADJ	39.84	quadratic	7.12
	50	elevation	66.43	quadratic	11.88
	70	coniferous	18.11	positive	3.16
	70	deciduous	34.00	positive	5.94
	70	PLADJ	53.27	quadratic	9.31
	70	elevation	12.53	quadratic	2.19

Continued on next page

Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
monthly					
	90	coniferous	27.33	positive	4.59
	90	deciduous	43.12	positive	7.24
	90	PLADJ	53.88	quadratic	23.06
biweekly					
	50	PLADJ	74.53	quadratic	8.19
	50	elevation	144.28	quadratic	15.85
	70	PLADJ	109.65	quadratic	12.48
	70	elevation	99.07	quadratic	11.27
	90	PLADJ	137.66	quadratic	16.10
	90	elevation	65.73	quadratic	7.68
weekly					
	50	PLADJ	100.94	quadratic	6.22
	50	elevation	289.42	quadratic	17.82
	70	PLADJ	185.51	quadratic	11.37
	70	elevation	208.63	quadratic	12.79
	90	coniferous	48.28	positive	2.97
	90	deciduous	120.49	positive	7.41
	90	PLADJ	172.50	quadratic	10.60
	90	elevation	57.75	quadratic	3.55

In roe deer the land cover type meadow was included in most models for both sexes and had a positive effect on home range size, but it affected the two sexes differently. Male roe deer show a higher explanatory value on larger spatial and temporal scales whereas females show a higher impact on core areas of the biweekly and weekly timescale. In addition to meadow the land cover types coniferous forest and deciduous forest had a positive relationship with home range size in both sexes but not on all spatio–temporal scale. Elevation showed an explanatory value for males with a positive relationship, except on the biweekly 90 % kernel. The climate variable precipitation had only an impact on females on biweekly and weekly timescales and temperature only on male roe deer on the monthly timescale.

Table 2: Summary of the back fitted t–values of the fixed effects for all mixed models of roe deer on all spatial and temporal scales. F–values and explained deviance (%) are shown retained from the mixed model, separated for males and females, with ID as random structure.

females					
Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
monthly					
	50	meadows	8.15	negative	4.19
	70	coniferous	0.85	positive	0.37
	70	deciduous	13.03	positive	5.65
	90	coniferous	1.67	positive	0.66
	90	deciduous	18.71	positive	7.34
biweekly					
	50	meadows	22.86	negative	5.14
	50	precipitation	5.18	negative	1.17
	50	PLADJ	29.63	positive	6.67
	70	meadows	25.33	negative	5.87
	70	precipitation	5.49	negative	1.27
	70	PLADJ	17.44	positive	4.04
	90	deciduous	11.27	positive	2.64
	90	meadows	19.75	negative	4.62
	90	precipitation	3.44	negative	0.81
	90	PLADJ	16.83	positive	3.94

Continued on next page

females					
Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
weekly					
	50	deciduous	17.32	positive	2.20
	50	meadows	43.98	negative	5.59
	50	precipitation	6.74	negative	0.86
	50	PLADJ	80.09	positive	10.18
	70	deciduous	19.54	positive	2.51
	70	meadows	45.25	negative	5.83
	70	precipitation	6.88	negative	0.89
	70	PLADJ	64.05	positive	8.24
	90	coniferous	1.18	positive	0.18
	90	deciduous	32.67	positive	4.91
	90	meadows	36.47	negative	5.47
	90	precipitation	7.32	negative	1.10
males					
Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
monthly					
	50	coniferous	9.19	positive	3.97
	50	meadows	9.69	negative	4.19
	50	temperature	5.77	positive	2.49
	50	elevation	6.56	positive	2.83
	70	deciduous	4.36	negative	1.74
	70	meadows	14.23	negative	5.69
	70	temperature	6.40	positive	2.56
	70	elevation	11.28	positive	4.21
	90	meadows	26.52	negative	8.55
	90	temperature	5.01	positive	1.61
	90	PLADJ	14.37	positive	4.63
	90	elevation	5.06	positive	1.63

Continued on next page

males					
Timescale	**Kernel size**	**Variables**	**F–value**	**relationship**	**expl.dev.(%)**
biweekly					
	50	meadows	16.72	negative	3.39
	50	PLADJ	35.68	positive	7.24
	50	elevation	6.59	positive	1.34
	70	coniferous	14.53	positive	2.98
	70	meadows	16.37	negative	3.36
	70	PLADJ	13.15	positive	2.70
	70	elevation	5.84	positive	1.20
	90	meadows	25.44	negative	4.79
	90	PLADJ	40.52	positive	7.64
weekly					
	50	coniferous	19.52	positive	1.67
	50	deciduous	10.37	positive	0.89
	50	meadows	29.46	negative	2.52
	50	PLADJ	55.18	positive	4.72
	50	elevation	18.18	positive	1.56
	70	coniferous	27.74	positive	1.96
	70	deciduous	11.82	positive	1.07
	70	meadows	34.44	negative	3.11
	70	PLADJ	41.37	positive	3.73
	70	elevation	16.16	positive	1.46
	90	coniferous	24.46	positive	2.35
	90	deciduous	12.99	positive	1.15
	90	meadows	36.03	negative	3.20
	90	PLADJ	38.88	positive	3.45
	90	elevation	8.12	positive	0.72

Table 3: Overview of AIC values for all mixed-models on all spatio–temporal scales. Models were fitted with and without spatial landscape configuration for both species, red (A) and row deer (B).

A **Red deer (*Cervus elaphus*)**

		Kernel size		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	with configuration	539.49	551.63	560.85
	without configuration	566.11	575.19	582.88
biweekly				
	with configuration	1065.20	1067.75	1066.00
	without configuration	1125.00	1129.57	1133.30
weekly				
	with configuration	1874.76	1862.45	1874.76
	without configuration	1986.64	1983.17	1986.64

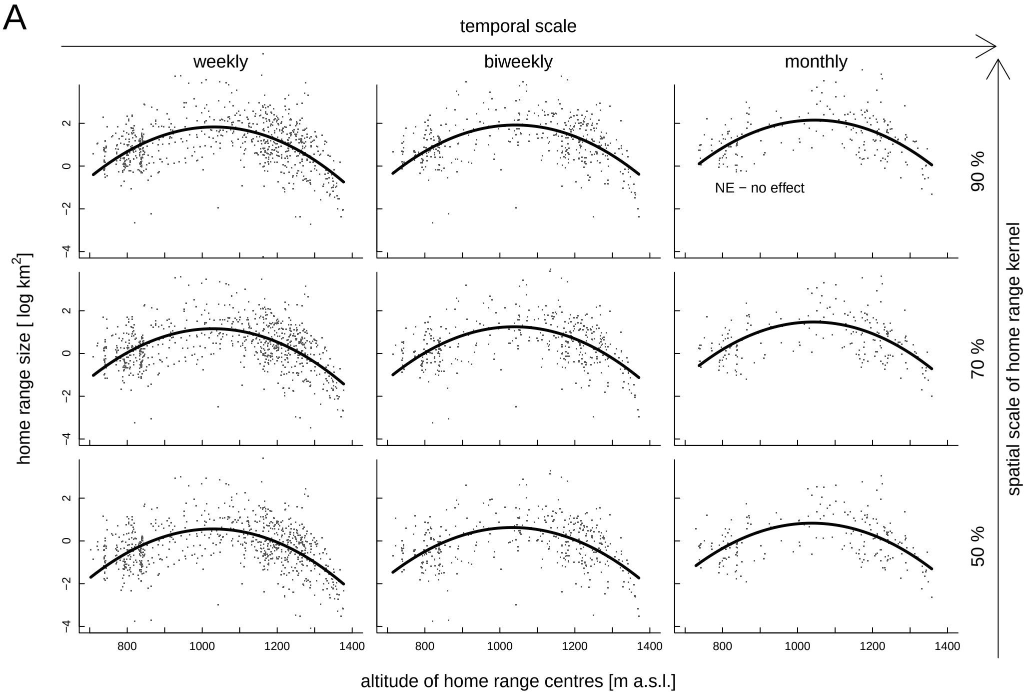
B **Roe deer (*Capreolus capreolus*)**

		Kernel size		
Timescale		**90 %**	**70 %**	**50 %**
monthly				
	with configuration	505.73	548.87	561.49
	without configuration	515.21	558.87	579.26
biweekly				
	with configuration	1102.28	1151.87	1160.83
	without configuration	1193.59	1248.23	1280.75
weekly				
	with configuration	2270.11	2275.87	2301.09
	without configuration	2355.88	2452.65	2520.21

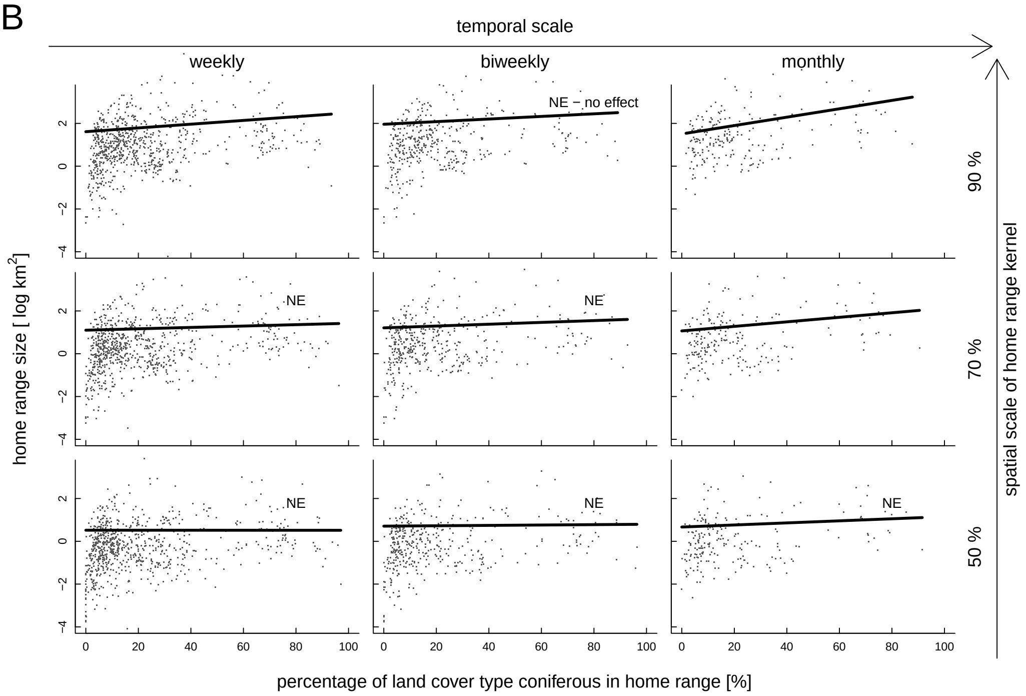
APPENDIX G:

Figures of fixed effects for the mixed models on all spatio–temporal scales for red and roe deer

Figure 1: Plot of log-transformed home range sizes (km^2) for red deer in relation to (A) altitude, (B) land cover coniferous forest, (C) land cover deciduous forest. Home ranges were calculated with the kernel method and the smoothing factor h on three isopleths (90 %, 70 %, 50 %) and three temporal scales (weekly, biweekly and monthly). Lines show predicted values of the mixed model and points raw residuals. Parameters with no explanatory value are marked with "no effect (NE)".



B


temporal scale
weekly
biweekly
monthly
NE − no effect
NE
NE
NE
NE
NE
home range size [log km^2]
spatial scale of home range kernel
90 %
70 %
50 %
−4
−2
0
2
0
20
40
60
80
100
percentage of land cover type coniferous in home range [%]

C

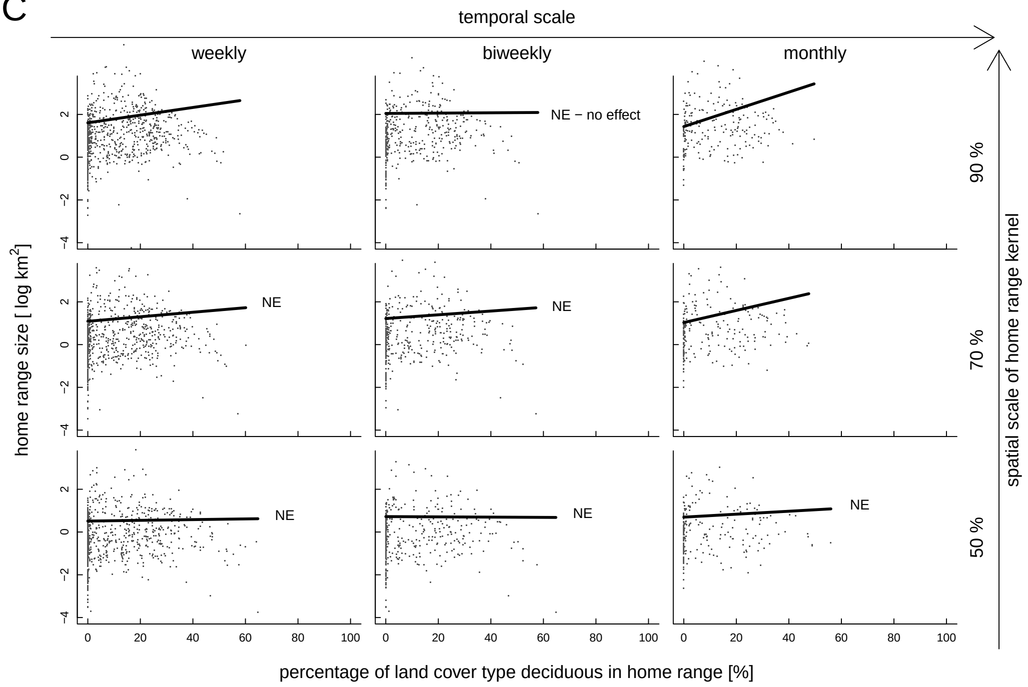
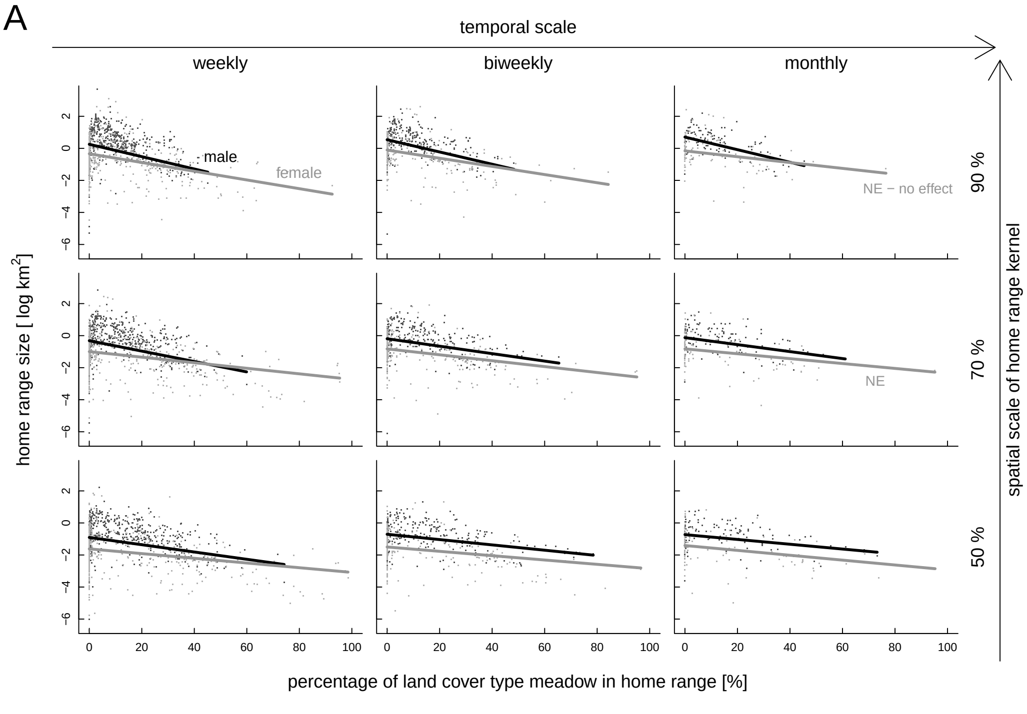
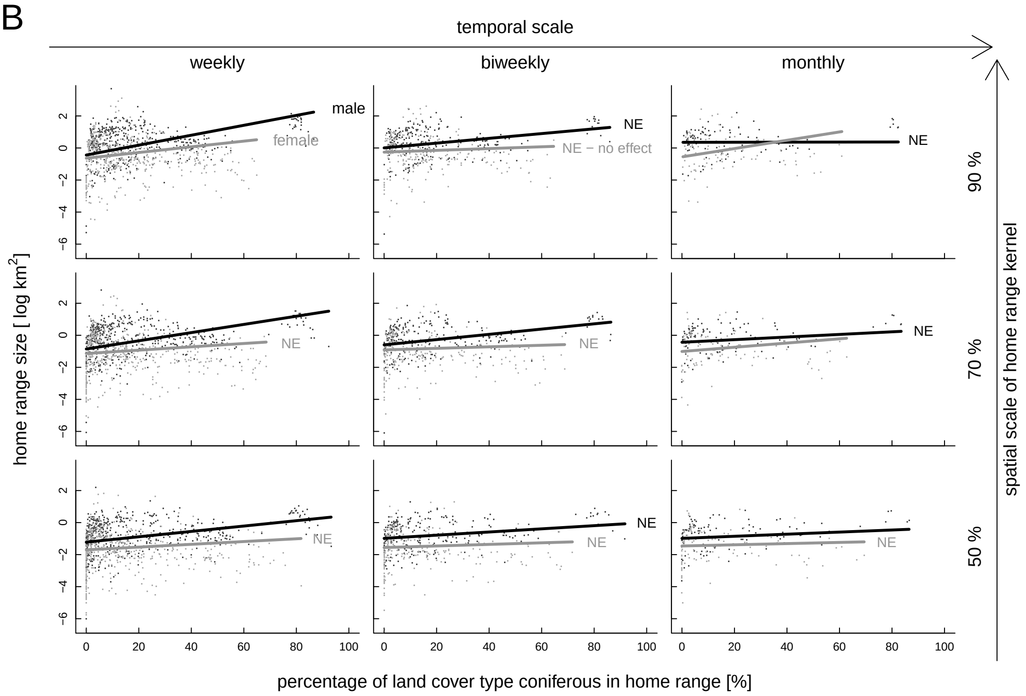

temporal scale
weekly
biweekly
monthly
NE − no effect
NE
NE
NE
NE
NE
home range size [log km^2]
spatial scale of home range kernel
90 %
70 %
50 %
−4
−2
0
2
0
20
40
60
80
100
percentage of land cover type deciduous in home range [%]

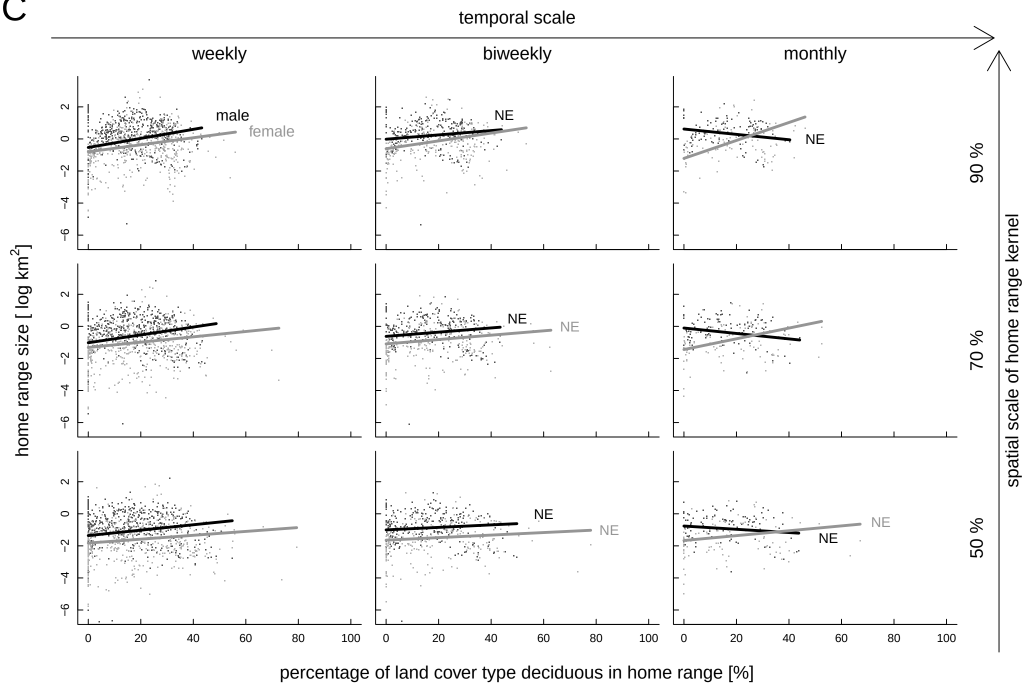
Figure 2: Plot of log-transformed home range sizes (km2) for female (gray) and male (black) roe deer in relation to (A) land cover meadow, (B) land cover coniferous forest, (C) land cover deciduous forest, (D) altitude, (E) precipitation and (F) temperature. Home ranges were calculated with the kernel method and the smoothing factor h on three isopleths (90 %, 70 %, 50 %) and three temporal scales (weekly, biweekly and monthly). Lines show predicted values of the mixed model and points raw residuals. Parameters with no explanatory value are marked with "no effect (NE)".



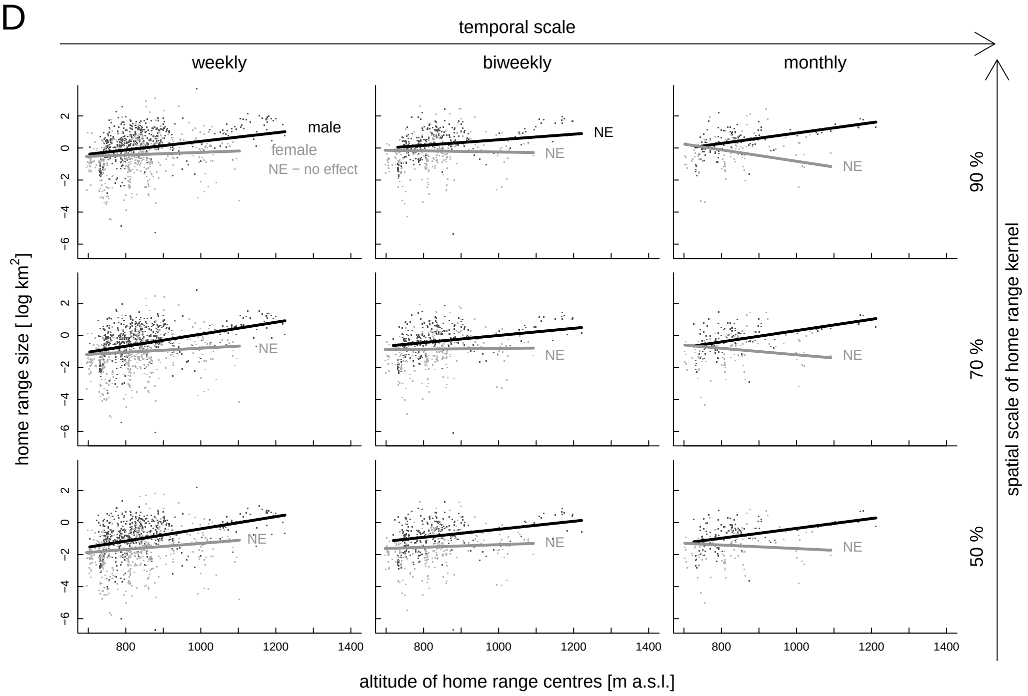
B


temporal scale
weekly
biweekly
monthly
male
female
NE
NE – no effect
NE
NE
NE
NE
NE
NE
NE
NE
NE
90 %
70 %
50 %
spatial scale of home range kernel
home range size [log km^2]
2
0
−2
−4
−6
0
20
40
60
80
100
percentage of land cover type coniferous in home range [%]

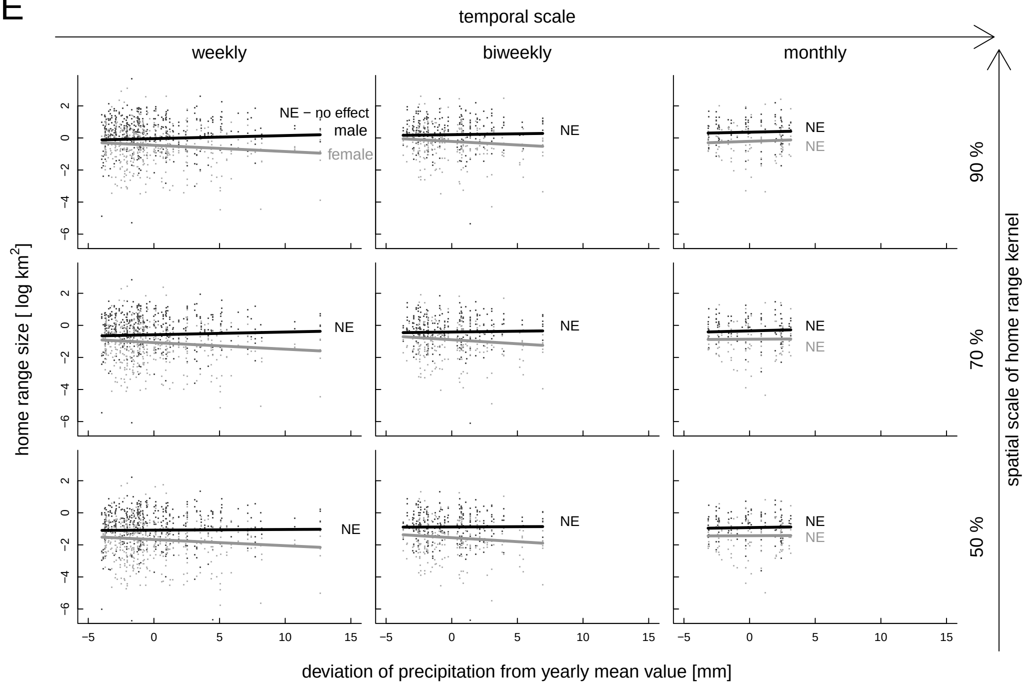
C


temporal scale
weekly
biweekly
monthly
male
female
NE
NE
NE
NE
NE
NE
NE
NE
NE
90 %
70 %
50 %
spatial scale of home range kernel
home range size [log km^2]
2
0
−2
−4
−6
0
20
40
60
80
100
percentage of land cover type deciduous in home range [%]

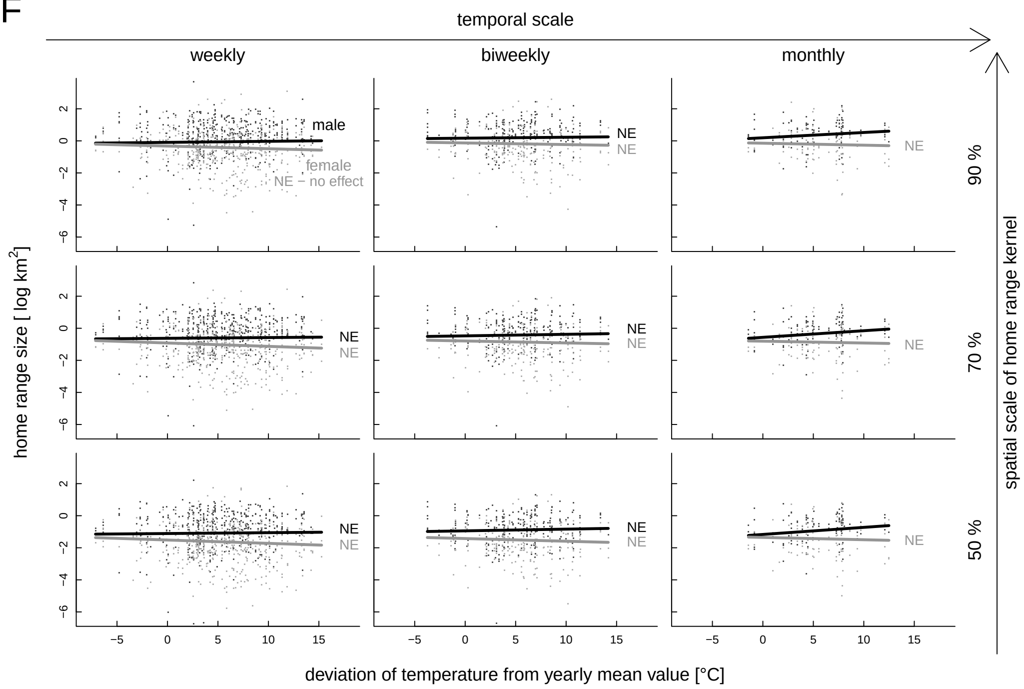
D


temporal scale
weekly
biweekly
monthly
male
female
NE − no effect
NE
90 %
70 %
50 %
spatial scale of home range kernel
home range size [log km^2]
2
0
−2
−4
−6
800
1000
1200
1400
altitude of home range centres [m a.s.l.]

E


temporal scale
weekly
biweekly
monthly
NE − no effect
male
female
NE
90 %
70 %
50 %
spatial scale of home range kernel
home range size [log km^2]
2
0
−2
−4
−6
−5
0
5
10
15
deviation of precipitation from yearly mean value [mm]

F

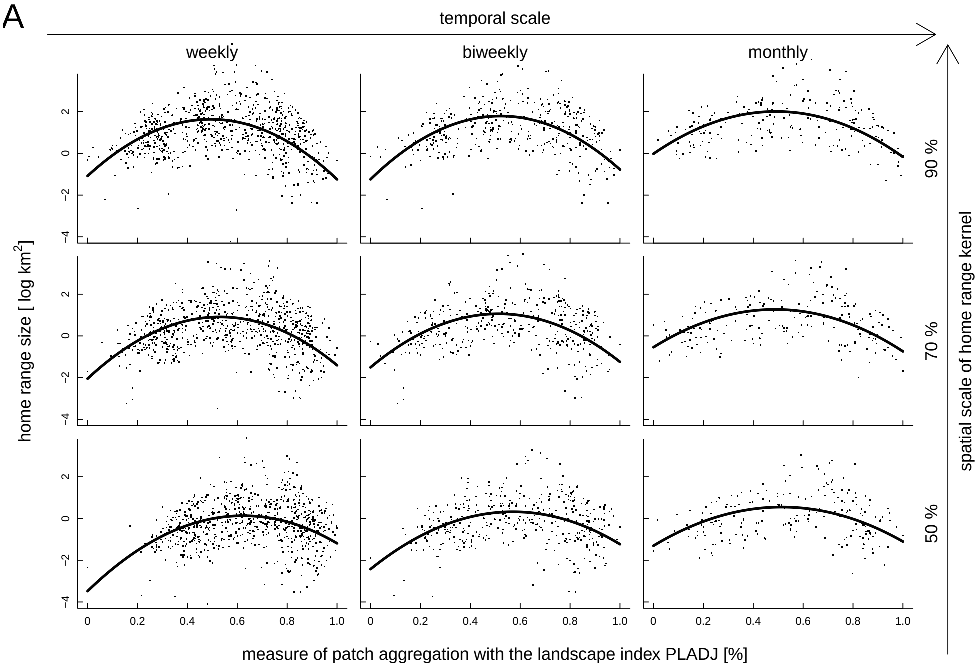

temporal scale
weekly
biweekly
monthly
spatial scale of home range kernel
90 %
70 %
50 %
home range size [log km^2]
male
female
NE − no effect
NE
2
0
−2
−4
−6
−5
0
5
10
15
deviation of temperature from yearly mean value [°C]

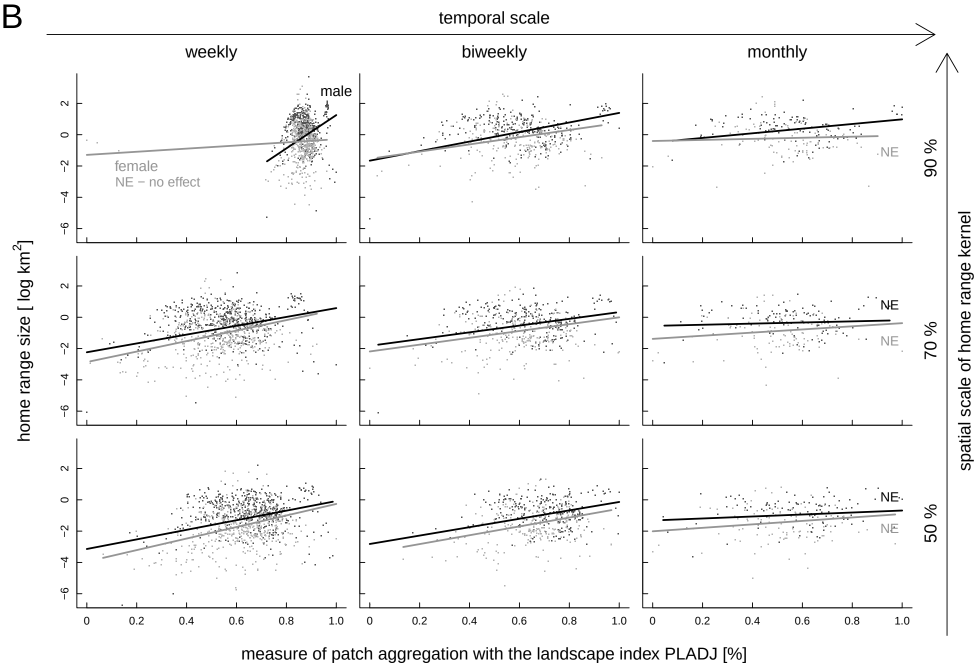
APPENDIX H:

Figures of home range sizes in relation to spatial configuration across spatio-temporal scales

Plot of log-transformed home range sizes (km^2) for red (A) and roe deer (B) in relation to the landscape index PLADJ calculated for each home range. Home range was calculated with the kernel method and the smoothing factor h. Estimates are given for the 90 %, 70 %, 50 % kernels and the weekly biweekly and monthly timescale. Lines show predicted values and points raw residuals.

A




B
temporal scale
weekly
biweekly
monthly
male
female
NE − no effect
NE
90 %
70 %
50 %
spatial scale of home range kernel
home range size [log km^2]
2
0
−2
−4
−6
0
0.2
0.4
0.6
0.8
1.0
measure of patch aggregation with the landscape index PLADJ [%]

Anlage 4:

Resource distribution explains temporal dynamics in habitat use by European roe deer

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Summary

1. One fundamental issue in animal ecology is understanding why animals select certain habitats. Habitat selection can be analysed at a very fine spatio-temporal resolution using GPS telemetry, which provides location data of cryptic organisms on almost continuous scale and airborne LiDAR (light detecting and ranging) and multispectral data, which provide detailed information about landscape properties.

2. The movement of an animal to a certain habitat is driven by landscape characteristics and the resource demands of the animals. Both vary over time, yet earlier studies on habitat use usually incorporated no time dependency or only on a very coarse scale. Huge amounts of fine-scale data can now be analysed by current statistical tools to determine site selection with respect to temporal variation.

3. Using generalized additive mixed effects models, we analysed the annual and diurnal habitat usage of 46 adult (≥ 2 years old) roe deer (*Capreolus capreolus*) with respect to land cover type and the availability of food and cover resources. Resource availability was obtained by LiDAR and biomass assay data.

4. Habitat usage varied strongly over both, annual and diurnal scales. Specifically, temporal variations of site selection could be explained by time-dependent variation of resource use. Model predictions revealed a trade-off in usage of the food and cover resources by roe deer that varied over time. The temporal variation of habitat use of females and males, however, did not significantly differ.

5. Our results exemplified a need for incorporating temporal dynamics in the analysis of habitat selection. Our study further showed the potential to understand habitat use based on continuous variables for resources and not based merely on habitat types, as has been done to date.

Key-words

land use; radio-tracking; sexual segregation; space use; resource selection; ungulate

Introduction

The access and range of resources vary over temporal and spatial scales. Animals therefore have to cope by adapting habitat selection to both their current demands and the spatial distribution of resources. The optimal time allocation to different habitat types results in a reasonably balanced utilization of resources for maximizing the success of survival, growth and reproduction.

Habitat selection has received much attention in the literature (e.g. Johnson 1980; Manly *et al.* 2002; Aarts *et al.* 2008). Even though it is well known that requirements of individuals of many species vary over different temporal scales, i.e. day and year (Börger *et al.* 2006; van Beest *et al.* 2011), studies have rarely considered a temporally dynamic calculation of habitat selection. An exception is a study of moose (*Alces alces)* (Bjorneraas *et al.* 2011), if seasonality was considered, separate models accounted for different seasons, e.g. for grizzly bears (*Ursus arctos*) (Nielsen *et al.* 2003); deer (*Odocoileus virginianus*)(Felix *et al.* 2007)and grizzly bears and cougars (*Puma concolor*)(Chetkiewicz & Boyce 2009). McLoughlin *et al.* (2010) emphasized that observations of temporal dynamics in resource selection have to be incorporated in the analysis of resource preference.

A considerable plasticity in the habitat selection of European roe deer has been observed but not fully understood (Morellet *et al.* 2011). Roe deer live in woods but are also widely distributed in fragmented and more open agricultural areas (Hewison *et al.* 2001). Roe deer are strongly attached to their home ranges and occupy the same site for many years (Linnel & Andersen 1995). Their habitat use has been intensively studied, and effects of habitat features on some life-history traits have been detected (Pettorelli *et al.* 2003; Nilsen, Linnell & Andersen 2004). Home range size is affected by various factors, e.g. habitat quality (Cibien & Sempere 1989; Tufto, Andersen &

Linnell 1996; Said *et al.* 2009) and sex. In general, males occupy larger home ranges than females (Cederlund 1983) and, the home range of females overlaps several male territories (Vanpe *et al.* 2009).

Many studies on the spatial behaviour of roe deer have differentiated between the sexes. Significant differences in spatio-temporal behaviour between females and males have been reported, e.g. time-budgeting (Turner 1979), home range size (Cederlund 1983), patterns in home range occupation (Bideau *et al.* 1993), spatial displacement after capturing (Morellet *et al.* 2009), and residence time in the summer range (Cagnacci *et al.* 2011). The results obtained indicate that it reasonable to distinguish between the sexes in the analysis of roe deer habitat use.

Despite the vast number of studies of the use of space by roe deer, only little is known about the rules governing roe deer movement behaviour (Coulon *et al.* 2008), including preference and avoidance of areas. Certain land cover types are visited more frequently than others relative to their proportional availability (Tufto, Andersen & Linnell 1996; Morellet & Guibert 1999). There are strong hints that roe deer behaviour changes monthly and diurnally (Turner 1978; Cederlund 1989; Pettorelli *et al.* 2005; Le Corre *et al.* 2008) and the composition of the roe deer diet varies seasonally (Cornelis, Casaer & Hermy 1999). However, studies on the variation in resource selection by roe deer have either not taken the temporal scale into account or only considered a coarse temporal scale, such as day/night or season (Mysterud *et al.* 1999; Mysterud, Lian & Hjermann 1999; Morellet *et al.* 2011).

Here, we adress this problem by analysing temporal variation of site selection with respect to categorical landscape variables, i.e. land-cover-types and continuous landscape variables, i.e. food and cover. We used generalized additive mixed effects models and included time as explaining variable over two temporal scales, annual and diurnal. We estimated food availability by means of biomass assay and vegetation cover in summer and winter using airborne LiDAR.

We expected 1) that the use of different habitat types by roe deer is subject to temporal fluctuations. We assumed that the analysis of temporal resource use would unravel the underlying causes of animal movement behaviour. Specifically, we expected 2) to find a trade-off in time allocation to food and cover resources over the course of a day in summer.

We hypothesized that differences in sociality of females and males would be reflected in different habitat usage. We expected 3) to see differences in the usage of land-cover types by females and males in the territorial phase (March/April-July) and the rut (July/August) but no differences during the rest of the time, when they partially form mixed-sex groups (Hewison, Vincent & Reby 1998). We assumed that females would prefer sites maximizing the chance of offspring survival, i.e. those relatively predator-safe and with sufficient food resources, and that males would select high-quality forage to enhance fighting ability and thereby increase their reproductive success.

Materials and methods

STUDY AREA

The study area is located in the Bavarian Forest National Park, which lies in south-eastern Germany along the border to the Czech Republic (49°30'19"N, 13°12'9"E).

The national park has three major forest types. Above 1,100 m a.s.l. (16% of the area), sub-alpine spruce forests of Norway spruce (*Picea abies*) and some mountain ash (*Sorbus aucuparia*) prevail. On the slopes between 600 m and 1,100 m a.s.l., mixed montane forests with Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*) (68% of the area) are found. In wet depressions in the bottom valleys (16% of the area), often associated with cold air pockets, spruce forests prevail with Norway spruce, mountain ash and birch (*Betula pendula*, *Betula pubescens*) (Heurich & Neufanger 2005). Since the mid-1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2011, this had resulted in the death of mature spruce stands over an area amounting to about 6,000 ha (Heurich *et al.* 2010; Lausch, Fahse & Heurich 2010).

Management of roe deer in the national park is spatially limited to the wild ungulate management zone. This management zone comprises approximately 20% of the study area and serves as a buffer zone in the transition area to the landscape surrounding the national park. This ensures that wildlife regulation measures are excluded from a core area of 20,000 ha (Heurich *et al.* 2011). The estimated roe deer population density was 1-3 animals/km^2 (M. Heurich *et al.* unpublished data). During our study, roe deer in the national park were subjected to predation by European lynx (*Lynx lynx*) which had been reintroduced in the 1980s (Woelfl *et al*. 2001).

Spectrozonal aerial images of the study area from 2008 (Heurich, Baierl & Zeppenfeld 2012) were used to classify forest areas according to the land cover (Belyaev *et al.* 2004). Images with a resolution of 0.4 m were used to isolate vegetation against the background of other underlying surfaces, different kinds of vegetation and different stages of vegetation of the same species (Belyaev *et al.* 2004). Land cover was grouped into 14 classes.

RESOURCE CLASSSIFICATION

Each land-cover type was assigned two resource values, one for forage availability and one for the degree of cover (Table 1). Cover values were estimated for leaf-off and leaf-on conditions from airborne LiDAR data acquired using a Riegl LMS-Q 560 system operating with a wavelength of 1,550 nm.

Leaf-off data were acquired between April 2008 and November 2009 from the entire national park area; data for the leaf-on area was acquired in May 2007 along four transects of approximately 400 m width, in total 16 km^2.

To estimate cover values, LiDAR points were first grouped into a 5×5 m grid. For each grid cell, we calculated inverse penetration ratios at a height of 0.5–2 m above ground, which represented an estimation of the fractional vegetation cover at this height (see Heurich & Thoma 2008 or Müller, Stadler & Brandl 2010 for more information). As the estimation of fractional vegetation cover directly above the ground is subject to errors due to imprecision of digital elevation models (Heurich *et al.* 2008), we did not include points below 0.5 m in the calculation.

The food index was based on estimations of herbaceous biomass realized by the model PhytoCalc (Bolte 2006; Heinrichs, Bernhardt-Römermann & Schmidt 2010). In this model, allometric equations relate plant species biomass to its cover and shoot length values. Cover and shoot length values were obtained from vegetation surveys conducted in June, July and August in 2009-2011 on 282 plots. Sampling design and coverage estimation are described in (Ewald *et al.* 2011). Shoot lengths of 20 individuals were measured for all species with coverage exceeding 1%. In all other cases, mean values of shoot lengths were taken from flora literature, i.e. Rothmaler (2005). As the PhytoCalc estimation is restricted to forest ground vegetation, the biomass of the herbaceous layer from cultivated and natural meadows was derived empirically by harvesting (4×1 m^2), drying (60 °C, 2 days) and weighing samples from 31 plots. Usually, there was more than one value for one land-cover type; for these, the median was calculated.

RADIOTELEMETRY

Global Positioning System (GPS) telemetry provided the data of 46 roe deer, recorded between winter 2005 and summer 2010. Each of the 24 males and 22 females were equipped with GPS-GSM collars (series 3.000) from VECTRONIC Aerospace, Berlin (Germany) and tracked over a period of about 3 months to almost 2 years.

The locations of the animals were recorded with different sampling intensities, ranging from every 3 min to every 12 h), but for the analysis, only one location per hour was kept to reduce spatio-temporal autocorrelation. We removed the first 10 days of each survey period to exclude a possible effect on behaviour owing to the capturing and handling of the animals (Morellet *et al.* 2009). This resulted in a total of about 82,400 records that were used for the analysis.

GPS radio-telemetry can be affected by imprecision and bias in locating animals (Stache, Löttker & Heurich 2012). In our study, spatial imprecision was negligible because the maximum error was about 15 m. The fixed rate, defined as the number of successfully stored locations divided by the number of attempts (Frair *et al.* 2010) for all animals was between 41 and 99% (mean 82%) and was uniformly distributed over day and year. Consequently, a relative effect on diurnal and monthly variations can be excluded.

STATISTICAL METHODS

Exploratory data analysis: resource selection indices

To visualize habitat selection over time, we calculated selection indices, i.e. the ratio %use/%availability for each land-cover type (Manly 1974; Arthur *et al.* 1996). A selection index of 1 corresponds to random selection; values > 1 indicate preference, and conversely, values < 1 indicate avoidance of the corresponding land-cover type. Selection indices were calculated for annual and diurnal time scales. The use/availability design requires the quantification of availability for each land-cover type (Johnson 1980). Here, we used the proportion of each land-cover type in the 95% home range of each individual, estimated using a Brownian bridge approach (Calenge 2006).

Models of resource and habitat selection

The use/availability design is intuitive and commonly used in the literature, but it is not appropriate for providing inference on population-level selection (Thomas & Taylor 2006), because the numbers of relocations differ among animals and over time.

To account for this, we modelled the temporal dynamics of habitat preferences of roe deer using binomial generalized additive mixed effects models (GAMMs). The dependent variable was the presence or absence of a particular animal in a given habitat at a specific hour of the day or month of the year. Each observation is represented by as many rows in the data frame as there are land-cover classes in the corresponding home range of the animal (typically 14, but sometimes fewer). We aimed to account for this inappropriately enlarged sample size by including observation weights, so that the sum of weights matched the original sample size.

Time as the main effect was modelled by a smooth non-parametric function, because we did not want to prescribe a prior particular functional relationship. We tested for differential use of habitats by the two sexes by comparing models that did not include terms for sex with models that included terms for sex. In the models for land-cover types, terms for sex included either as a main effect of sex or as interactions with the main effects of land-cover types. In the more complex version, interactions between sex and the smooth term for time were modelled so that separate temporal dynamics of habitat preference were fitted for each sex. In the most complex version, food and cover were modelled as continuous variables, as a tensor product of an isotropic 2-D tensor product smooths with a cyclic 1-D (and also 2-D) smoothing in time. Predictions of the model smoothed over the diurnal scale were performed only for data from May, June and July as resource values were available only for these months. Smoothness selection was controlled by using maximum-likelihood criteria which are less prone to local minima and are therefore more robust.

The availability of a given land-cover type, i.e. the fraction of the area covered by this land-cover type, varied across the home ranges of different animals. To account for this, the logit of the availability of a land-cover type within the corresponding home range of the animal was included as an offset term – a constant term in the model equation with an associated parameter fixed at 1.

Variation in selection preferences across animals and years were accounted for by including random effects for individuals as well as years integrated in the model as penalized regression terms.

The GAMMs of the land-cover type provided predictions of relative usage given specific values for time of the day and/or year and the availability of land-cover type. The latter was set to the mean value of all animals for the corresponding land-cover type. Realizations of variables of random effects were not factored in the predictions.

All analyses were conducted in R version 2.15.2 (R Development Core Team 2012) on a Linux 64-bit system using packages mgcv version 1.7-22. (Wood, 2006) for GAMMs and adehabitatLT version 0.3.5 for home range calculations (Calenge 2006).

Results

PATTERNS OF HABITA SELECTION ACCORDING TO LAND-COVER TYPE

As expected, our analysis revealed a temporal variation of habitat use by roe deer (Figs. 1, S1). Basically, three types of variation on daily usage could be detected. Roe deer selected medium-aged and mature coniferous stands (Figs. 1, S1), medium-aged deciduous and mixed stands, and standing and lying dead wood more often during the day than at night. At all times, coniferous stands and dead wood areas were avoided (selection index (SI) < 1), whereas medium-aged deciduous and mixed stands were preferred (SI > 1). Roe deer used mature mixed stands almost constantly and slightly more often at dusk and dawn. The animals showed no particular preference for mature stands (SI≈1 for the whole day) but a considerable preference for young mixed stands (SI >> 1). The animals also constantly used clear-cut areas, which were slightly preferred (SI > 1), and mature deciduous stands, which were selected rather randomly (SV ≈ 1). Built-up areas were totally avoided during the day and avoided to a lesser extent at night. Transition stands between forest, meadow and line vegetation, and cultivated and natural meadows (Fig. 1) were highly preferred (SI >> 1) at night and preferred to a lesser extent or even avoided (cultivated meadows, SI < 1) during the day. Absolute selection indices calculated by GAMMs have to be treated with caution, because predictions were divided by the mean relative availability of the land-cover type for all animals. This explains why predicted curves and the median of the %use/ %availability approach differ for some land cover types (e.g. young mixed stands in Fig. 1).

Patterns of variation of usage on the annual scale exhibit four types (Figs. 2, S2). In winter, they more often selected built-up areas, old coniferous and mixed stands. In summer, they more often selected medium-aged coniferous and deciduous stands, lying dead wood, meadows, young mixed stands and transition stands between forest, meadow and line vegetation. They selected medium-aged-mixed stands and standing dead wood constantly throughout the year and preferred clear-cut in autumn, and mature deciduous stands in spring and autumn.

PATTERNS OF HABITA SELECTION IN CONTINUOUS RESOURCE SPACE

As expected, continuous variables for resources explained the temporal variation in habitat use in the various models (Table 2). Model L0, based only on land-cover types, was equivalent to CF0, based only on resources, and resulted in same values for the proportion of the null deviance explained by the model. The explained deviance can be increased if time-dependent resource values are used (different values for cover in summer and winter) instead of constant resource values, as exemplified in Model CF1. This demonstrates that time-dependent resource values would better fit such models. The inclusion of time in models CF2, CF3, CF4, L2, L3 and L4, resulted in a better fit, but the explained deviance was considerably higher, as was the adjusted R^2 which takes the number of predictors into account. The relatively low explained deviance for Model L1 compared to models with a smoothing for time demonstrated that a smooth function is the better choice for modelling time-dependent variation of usage. Models CF3 and L3 use *month* as the smoothed predictor variable and provided almost the same proportion of deviance explained, whereas Model L3 reached a slightly higher value since this model is more flexible as time-dependent selection was modelled for each land-cover type separately. The higher flexibility resulted in a higher value for estimated degrees of freedom (edf). Models containing *hour* as explanatory variable in the smoother reached a higher explained deviance if modelled with continuous variables for food and cover (Model CF2). The higher explained deviance required a higher number of edf compared to Model L2. If *month* and *hour* are included, the model for land-cover types (Model L4) results in a higher explained deviance even with edf lower than in the model with continuous variables (Model CF4).

When sex as the linear predictor and its interaction with land-cover type were included, all models had a higher explained deviance and higher edf. But for all models, all terms including sex are not significant (neither the single linear predictor nor the interaction with land cover type, Table 3).We therefore conclude that sex as a linear predictor does not improve the model.

The probability of resource usage over time of the day in summer (May–July) was calculated given a relative frequency of 0.2% (arbitrarily chosen) of the respective resource category (Fig. 3). A considerable preference towards sites providing high cover and low food availability throughout the day was revealed, with an even stronger selection during daylight hours. Sites characterized by low cover but high food availability were selected conversely, with a strong preference during the night and almost avoidance during the day. Sites with a medium food availability and cover were rather randomly chosen, with no particular preference or avoidance at any time. However, sites providing a very food availability and cover were less frequently selected as expected if animals chose sites randomly.

SEXUAL SEGREGATION

Contrary to our expectation, in models including an interaction term of land-cover type and sex, the usage of land cover type by females and males in general did not significantly differ , not even if temporal variation over both time scales was included

(Table 3). On the diurnal scale (Model L2_S in Table 3), the lowest p-values were found for young mixed stands (0.07) and medium-aged deciduous stands (0.08), which implied a reasonably but not significant differential usage of these land-cover types throughout the day by both males and females. Differences in usage of land-cover type on the annual scale also did not significantly differ between sexes (Model L3_S in Table 3). Only the selection of young mixed stands differed to a great extent (0.008), and the selection of mature coniferous stands differed with low significance (0.09). We found also no significant differences between the sexes when the models were calculated for each month separately (not shown).

Discussion

PATTERNS OF HABITA SELECTION ACCORDING TO LAND-COVER TYPES

Our models indicated basically three types of temporal variation in the usage of land-cover types by roe deer (Fig. S3): mostly variation over the annual scale (mature deciduous stands, mixed young stands, transition stands, clear-cut and lying dead wood), mostly variation over the diurnal scale (medium-aged coniferous stands and medium-aged mixed stands, standing dead wood and built-up areas) and variation over both scales (medium-aged deciduous stands, mature mixed stands and mature coniferous stands and cultivated and natural meadows).

The usage of medium-aged mixed stands varied mainly over the diurnal scale, usage of mature and young mixed stands varies mostly over the annual scale but to opposite extents. The observed annual variation resembled the seasonal differences of conditions inherent to the stands. For example, undergrowth in young stands provides cover and optimal forage for roe deer with, e.g. mountain ash, and is therefore favoured in summer (Barranceková *et al.* 2010; Fielitz & Albers 1996). In general, the usage of medium-aged stands varied over the course of the day, with a preference during daylight hours, most likely beacause these sites with natural undergrowth provide shelter and food. Only for medium-aged deciduous stands did the variation occur also over the annual scale, which can be explained by the great changes in conditions in deciduous stands over the course of the year. Also the annual usage of mature deciduous stands greatly varied. In the leaf-off period, these stands were avoided, probably because the area was covered with snow which would result in a higher expenditure of energy when foraging or travelling. These stands were preferred only in spring and autumn; in spring, the undergrowth supplies much highly nutritious food (Marell, Archaux & Korboulewsky 2009), and in autumn, high-energy beechnuts are provided (Olesen & Madsen 2008). Mature stands were in general avoided in summer probably because tof the sparse undergrowth with a low availability of nutritious forage, caused by the low transmission of light . Mature coniferous stands and mature mixed stands, were preferred during winter months especially by females; these stands provide cover from snow and harsh weather conditions.

Open habitats were extensively used during the summer months; these sites offer highly nutritious forage. These sites are avoided in winter probably because animals would be more highly exposed to wind and precipitation and these areas are covered with snow, which would hinder animals in their search for food.

Clear-cut areas were visited frequently, probably because the opening of the forest canopy results in a stronger growth of ground vegetation and therefore plenty of food. These sites, however, provide hardly any cover, and we would have expected that such sites would be avoided during the day, which was not the case.

Although areas with lying dead wood – a consequence of the bark beetle outbreak – would provide a good amount of biomass in summer,these areas are avoided. The explanation that lying trunks and branches would hinder the movement of roe deer is is supported by an analysis on habitat selection of red deer (*Cervus elaphus*) where it was shown that also red deer avoided lying dead wood (C. Dupke *et al*, unpublished data).

Cimino & Lovari (2003) found that changes in the availability of cover and food results in shifts of home ranges, particularly for female roe deer. Hence, variation in habitat usage over the course of the year, as observed in our study, can be explained by the different characteristics of the habitat types in providing shelter from various weather conditions and the varying availability of forage over the course of the year.

Diurnal variations are mainly driven by daylight and the spatio-temporal heterogeneity in disturbance and predation risk. In open areas, animals may be disturbed by human activity; these areas are therefore avoided during the day and preferred at night (Herbold 1995). Meadows provide an optimal site during the night, when lynx usually hunt (Podolski *et al.* 2012), as roe deer can forage and minimize predation risk by the high visibility over the area. In fact, visibility has been found to be the most relevant factor in the vulnerability of offspring (Panzacchi *et al.* 2010). During the day, roe deer prefer habitat types that provide cover. Hiding behaviour usually occurs in places frequently visited by humans (Herbold 1995). Even though roe deer has not been subjected to management interventions the deer still avoid human contact.

Earlier studies have concentrated on a rather rough division of landscape types (e.g. Morellet *et al.* 2011). Our analysis exemplifies that grouping land-cover types only according to tree species composition is not appropriate if the interest lies with habitat usage. For all forest stand compositions, i.e. coniferous, deciduous and mixed, different stand age classes were used by roe deer at different times. Hence, both stand age class and tree species composition together are a better proxy for understanding habitat usage.

PATTERNS OF HABITA SELECTION IN CONTINUOUS RESOURCE SPACE

Our results showed that throughout the day, roe deer favour sites that provide cover, whereas at night they prefer foraging sites that provide much biomass; these results support the results of an earlier study (Benhaiem *et al.* 2008). Roe deer apparently balance between the usage of food resources and cover, and this trade-off appears to be ruled by daylight. Earlier studies, that focused on one single resource have reported that roe deer select sites either for maximizing food intake (Mysterud, Lian & Hjermann 1999; Pellerin *et al.* 2010) or for reducing predation risk (Linnell, Nilsen & Andersen 2004; Bongi *et al.* 2008; Panzacchi *et al.* 2010). Sites that are attractive for foraging may be associated with a higher predation risk, which leads to a trade-off between food and risk avoidance (Houston, McNamara & Hutchinson 1993).

SEXUAL SEGREGATION

The observed weak differentiated usage of land-cover types by females and males was insufficient to support our initial hypothesis that in summer females use relatively predator-safe sites more intensively than males. Our results supported earlier studies on sexual segregation of ungulates that suggested that roe deer, as an ungulate with a slight size dimorphism, exhibits only limited sexual segregation (Mysterud, Lian & Hjermann 1999; Bonenfant *et al.* 2007; Morellet *et al.* 2011). According to the forage selection hypothesis (Ruckstuhl & Neuhaus 2002), female and male roe deer would not use space differentially because of their slight size dimorphism (Andersen *et al.* 1998), as found in studies that compared sexual segregation among ungulates (Bonenfant *et al.* 2007; Morellet *et al.* 2011). Sexual segregation increases with increasing levels of body size dimorphism between the sexes, as shown by a comparative study of 40 species of large herbivores (Mysterud 2000). In contrast, Mysterud, Lian & Hjermann (1999) reported sexual segregation of roe deer in winter.

Earlier studies have also demonstrated that female roe deer, known as “income breeders”, afford a high level of energy for prenatal and postnatal care in spring and summer (Andersen *et al.* 2000), which results in a higher selection of habitat types that grant the highest energetic gain (Panzacchi *et al.* 2010). This is reasonable because fawn survival highly depends on maternal energetic constraints McLoughlin *et al.* (2010). Our analysis revealed that site selection of females did not differ from that of males, which suggested that males have an equally high demand of energy intake during the summer. One reason might be the higher energy needed for defending the territory.

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Table 1. Overview of land cover types. Cover values are relative to each other during the respective season; absolute values should not be compared between summer and winter.

Land-cover type	Relative frequency	Biomass (g/m^3)	Cover summer	Cover winter
Built-up areas	0.016	89	0.27	0.097
Clear-cut areas	0.047	122	0.77	0.43
Coniferous stand, mature	0.21	83	0.43	0.29
Coniferous stand, medium-aged	0.035	66	0.899	0.67
Deciduous stand, mature	0.19	1	0.27	0.19
Deciduous stand, medium-aged	0.014	56	0.71	0.28
Lying dead wood	0.091	187	0.61	0.66
Meadows, cultivated	0.054	299	0	0
Meadows, natural	0.014	90	0.45	0.32
Mixed stand, mature	0.224	25	0.23	0.13
Mixed stand, medium-aged	0.037	65	0.83	0.897
Mixed stand, young	0.01	50	1	1
Standing dead wood	0.026	172	0.34	0.22
Transition stands between forest and meadows and line vegetation	0.006	90	0.82	0.98

Table 2. Overview of models. Summary of generalized additive/linear mixed effects models for predicting the probability of site selection. Fixed effects of the models are shown in the first column. All models include the same random effects: ID of individual and year. Furthermore the logit of the relative availability of the respective land cover type was included as the model's offset. Abbreviations: coverS, cover in summer; coverW, cover in winter; coverWS, cover in winter and summer (value depends on time of position recording); food, value of food abundance at a site ; LC, land- cover type; s, smooth term; te, tensor product smooth term; by, a replicate of the smooth is produced for each factor level of LC; edf, estimated degrees of freedom . When a spline function are used as an estimator, the degrees of freedom have to be estimated, based on the number of parameter, constraints and smoothing parameter.

Model	Predictive variables of the fixed effects	R^2 (adjusted)	Explained deviance	edf
L4_S	te(month, hour, by = LC) + LC*sex	0.125	20.0	122.1
L4	te(month, hour, by = LC) + LC	0.122	19.7	80.38
L3_S	s(month,by=LC) + LC*sex	0.116	18.91	78.48
L3	s(month,by=LC) + LC	0.113	18.53	64.31
L2_S	s(hour,by=LC) + LC*sex	0.109	18.14	63.63
L2	s(hour,by=LC) + LC	0.106	17.82	49.97
L1	hour*LC+month*LC	0.101	16.7	43.75
L0	LC	0.097	16.3	14.9
CF4	te(coverWS, food, month, hour)	0.1199	19.0	134.2
CF2	te(coverWS, food, hour)	0.1159	18.56	57.43
CF3	te(coverWS, food, month)	0.1128	18.35	58.8
CF1	te(coverWS, food)	0.107	17.2	22.04
CF0	te(coverS, food) & te(coverW, food)	0.097	16.3	14

Table 3. Summary statistics for models L2_S, L3_S and L4_S. The first two columns of each model refer to the significance of the effect of sex and the interaction between sex and the land-cover type (LC). For all models the effect of sex were not significant (except from young mixed stands in L2_S). The third and fourth columns show the significance of the respective smooth term over time for each land cover type. The higher the edf (>1) the stronger the smooth differs from a straight line. p-values for the smoothers have to be treated with caution.

	Model L2_S				Model L3_S				Model L4_S			
	s(hour,by=LC) + LC*sex				s(month,by=LC) + LC*sex				te(month, hour, by = LC) + LC*sex			
	Estimate	Pr(>|z|)	edf	p-value	Estimate	Pr(>|z|)	edf	p-value	Estimate	Pr(>|z|)	edf	p-value
sex_male	-0.08	0.84			0.28	0.48			0	0.99		
Land-cover type	Sex:LC		s(Hour):LC		Sex:LC		s(Month):LC		Sex:LC		te(Hour,Month):LC	
Built-up areas			1.98	0.004			1.69	0.025			2.85	0.006
Clear-cut areas	-0.08	0.85	0.11	0.852	-0.42	0.31	2.23	<0.001	-0.13	0.77	2.40	0.0014
Coniferous stand, mature	-0.20	0.62	2.93	<0.001	-0.68	0.09	3.77	<0.001	-0.30	0.49	9.24	<0.001
Coniferous stand, medium-aged	0.80	0.11	2.01	0.003	0.40	0.42	0.82	0.189	0.72	0.18	3.37	0.007
Deciduous stand, mature	0.19	0.63	0.08	0.910	-0.08	0.84	4.40	<0.001	0.15	0.74	3.68	0.0047
Deciduous stand, medium-aged	0.77	0.08	1.46	0.045	0.33	0.46	1.89	0.007	0.72	0.13	3.46	0.012
Lying dead wood	0.50	0.29	1.68	0.025	0.21	0.65	3.51	<0.001	0.51	0.30	6.10	<0.001
Meadows, cultivated	0.41	0.32	4.19	<0.001	0.11	0.78	3.46	<0.001	0.38	0.39	10.80	<0.001
Meadows, natural	0.65	0.13	3.14	<0.001	0.32	0.45	3.97	<0.001	0.56	0.22	9.15	<0.001
Mixed stand, mature	-0.19	0.64	1.50	0.077	-0.55	0.17	4.71	<0.001	-0.30	0.50	7.48	<0.001
Mixed stand, medium-aged	0.21	0.61	2.61	<0.001	-0.13	0.75	0.08	0.965	0.13	0.77	2.43	<0.001
Mixed stand, young	-0.81	0.07	0.13	0.537	-1.20	0.01	3.37	<0.001	-0.87	0.07	2.76	<0.001
Standing dead wood	-0.10	0.82	2.50	<0.001	-0.57	0.19	1.55	0.056	-0.17	0.72	2.51	<0.001
Transition stands between forest and meadows and line vegetation	-0.01	0.99	1.05	0.130	-0.35	0.47	2.22	<0.001	-0.07	0.90	2.17	<0.001

Figures

Fig.1. Selection of the habitats mature coniferous, mature mixed stands and cultivated meadows varying over the course of the day. Boxplots show the distribution of selection indices for 46 roe deer (24 male, 22 female): Selection index is the quotient of relative usage and relative availability of the respective land cover type for an individual. A value of greater than 1 indicates preference of the habitat type for a particular time, a value less than 1 avoidance. Red lines denotes the selection value predicted by the GAMM ((predicted relative usage)/(mean value of availability for all animals)) with the IDs of roe deer and year as random effect. The orange shading represents the estimate of the 95% confidence interval.

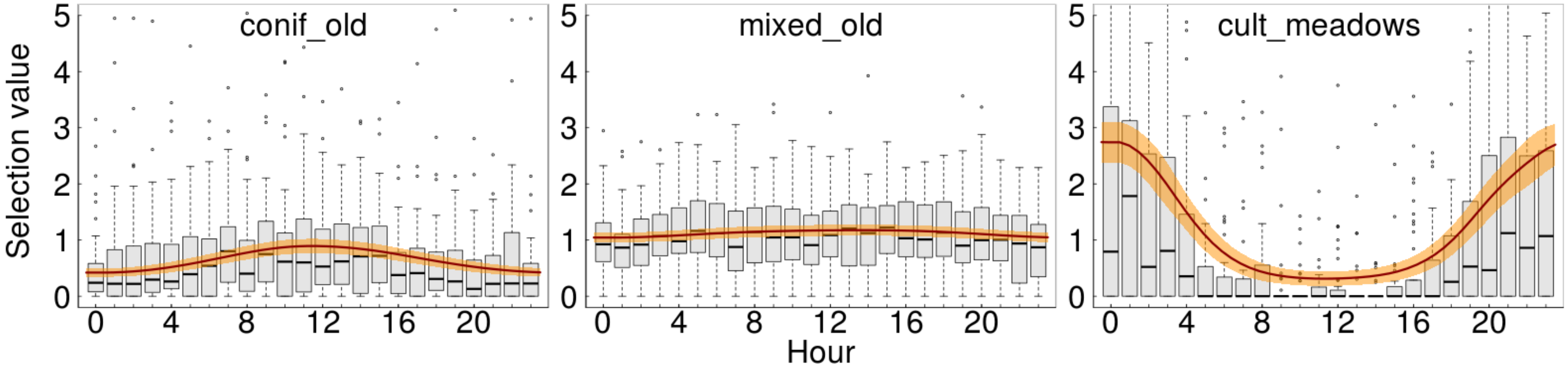


Fig. 2: Variation of selection of mature mixed stands, cultivated meadows and young mixed stands with respect to time of the year for all 46 roe deer. Boxplots show the distribution of selection indices. The red and blue line correspond to the selection index predicted by the GAMM (predicted relative usage/mean value of availability for all animals), with the individual roe deer and year as random effects. Orange shading represents the estimate of the 95% confidence interval. Note the different scaling of the y-axis in the third plot.

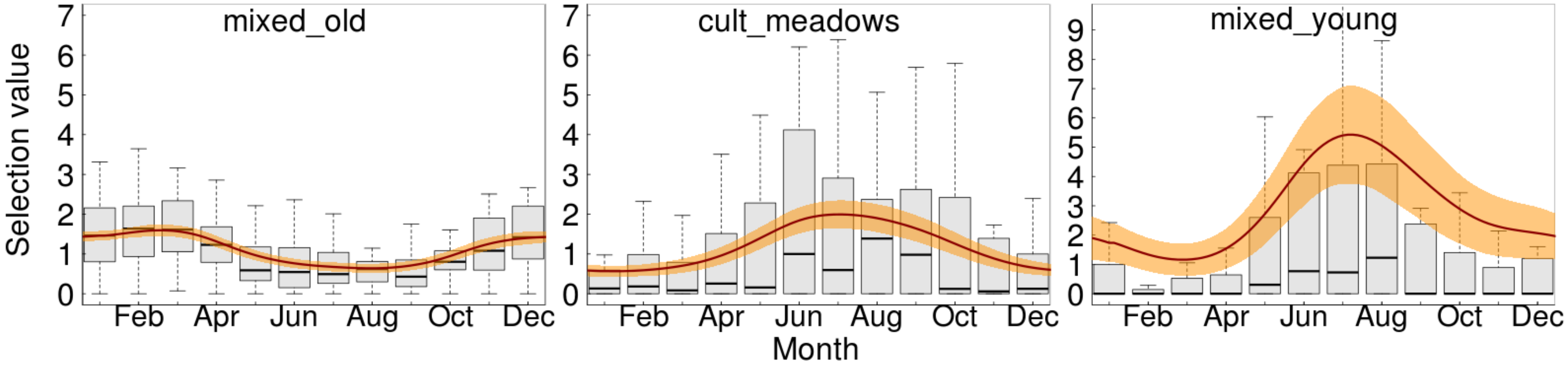
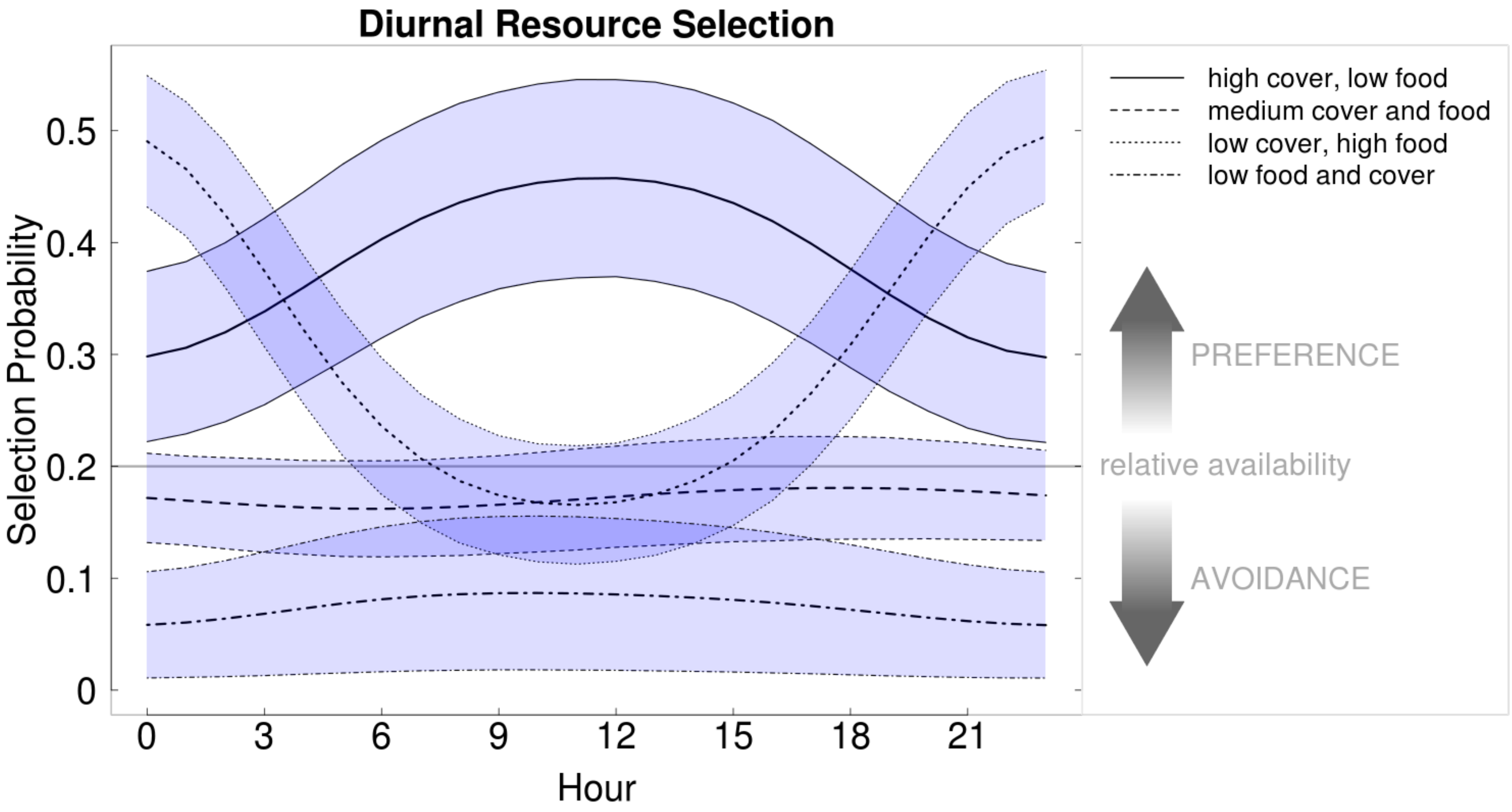


Fig. 3. Predicted selection probability of sites with a given resource availability in a possible range between 0 and 1 for all roe deer in summer (June, July, August), given a relative availability of 0.2 (arbitrarily chosen) for each site. Solid line: high cover (0.9) and low food (0.1); dashed line: medium cover (0.5) and medium food (0.5); dotted line: low cover (0.1) and high food (0.9); dash-dotted line: low cover (0.1) and low food (0.1). Predictions are based on GAMMs, including time of the day (hour), the resources food and cover, random effects of individuals and year, and the logit of the relative availability of the resources as the model offset modelled as a tensor product of an isotropic 2-D tensor product smoothing with a cyclic smooth in time (estimated degrees of freedom = 30.9, p-value < 2*10–16). Shading corresponds to the 95% confidence interval.


Diurnal Resource Selection
Selection Probability
0.5
0.4
0.3
0.2
0.1
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3
6
9
12
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Hour
high cover, low food
medium cover and food
low cover, high food
low food and cover
PREFERENCE
relative availability
AVOIDANCE

Supporting Information

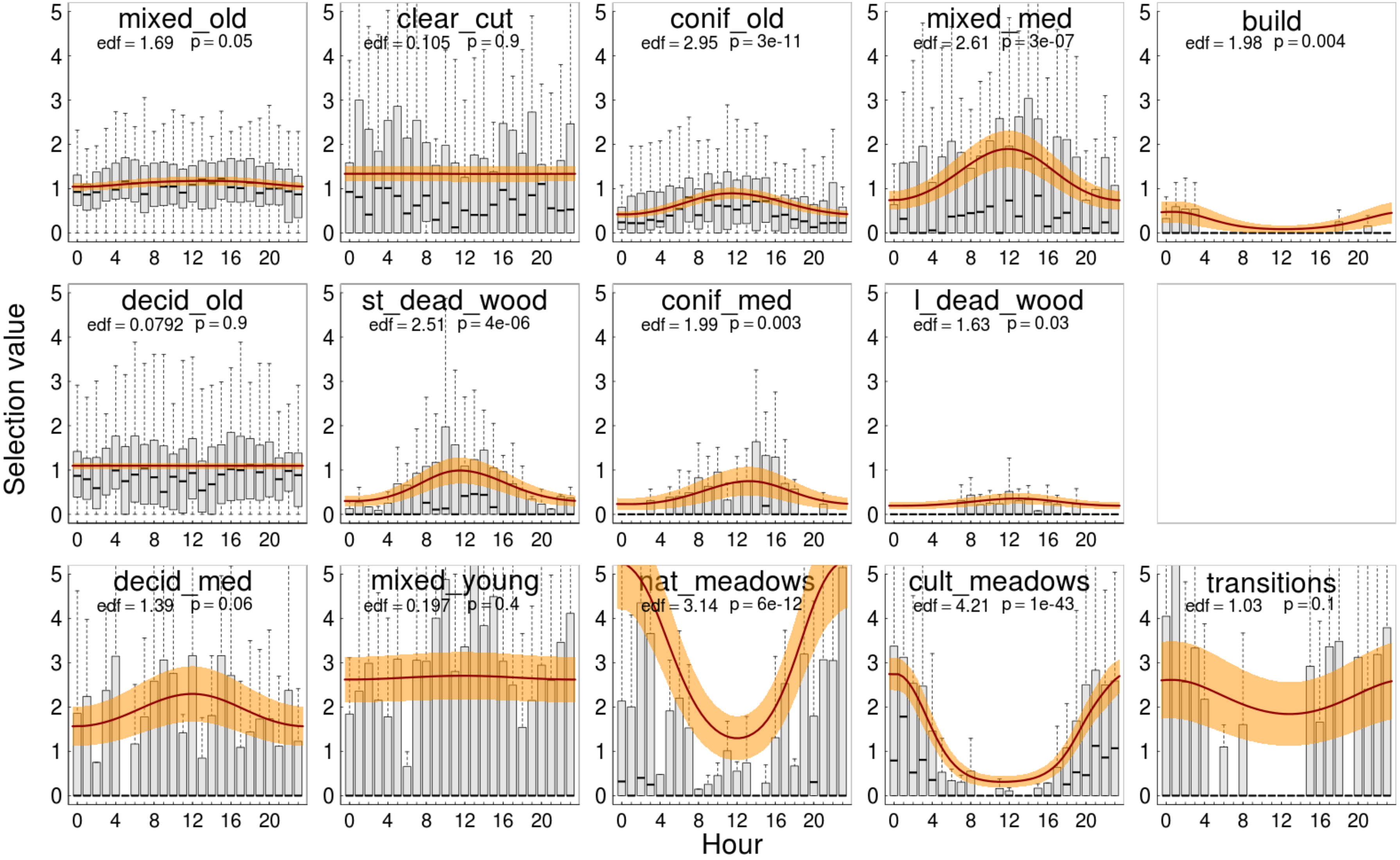

Fig. S1. Plots of selection indices varying over daytime for all land cover types. Boxplots show the distribution of selection indices for 46 roe deer (24 male, 22 female); outliers are not drawn. The selection index is the quotient of relative usage and relative availability of the respective land cover type for an individual. Red lines indicate the prediction of the GAMM with the individual roe deer as random effect. The orange shade represents the estimate of the 95% confidence interval. Estimated degrees of freedom (edf) and p-values based on F-tests provide a rough guide to the significance of the smoother: the higher the edf (>1) the stronger the smooth differs from a straight line.

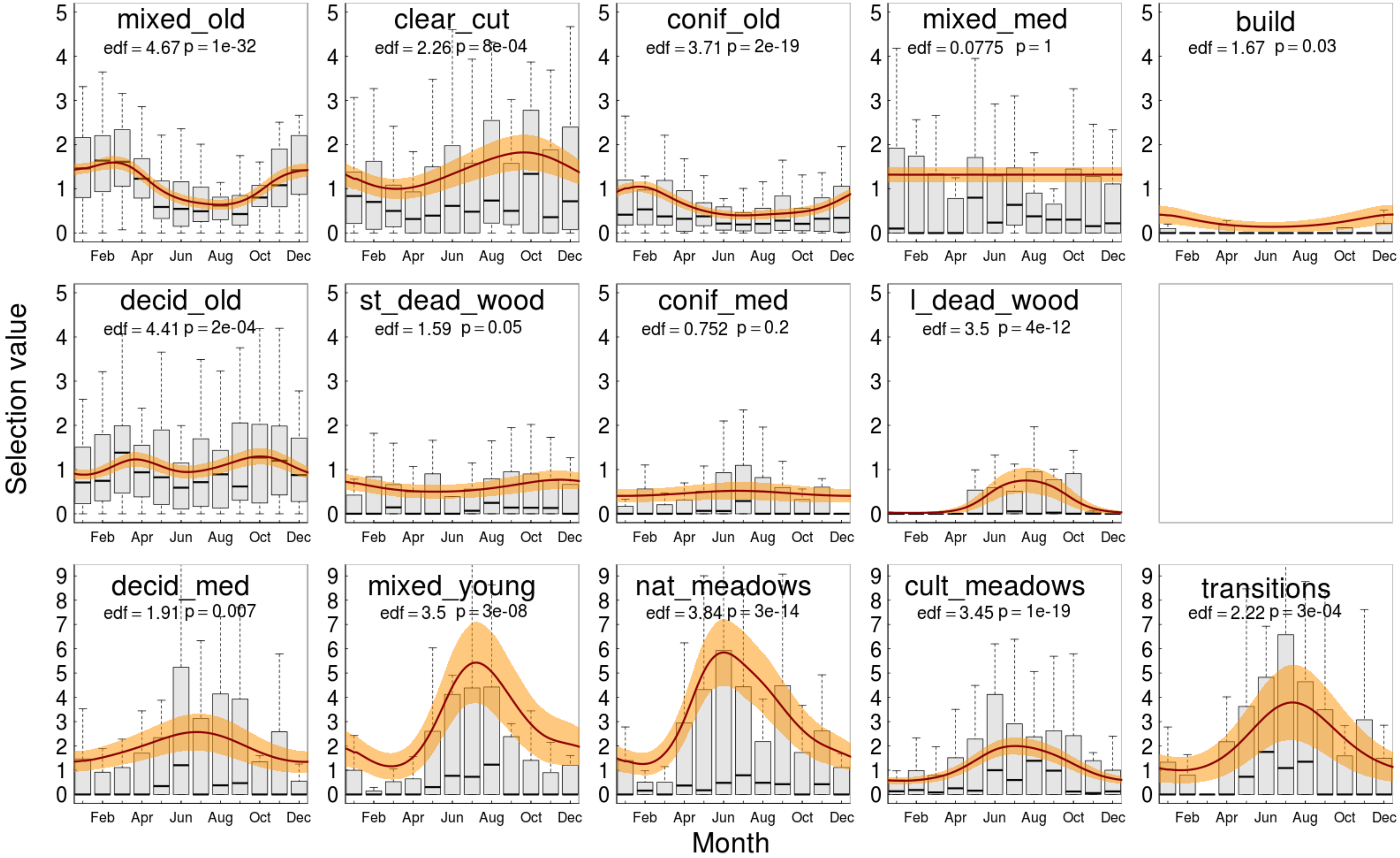

Fig. S2. Variation of selection with respect to time of the year for all roe deer and for all land cover types. Boxplots show the distribution of selection indices for 46 roe deer (24 male, 22 female). The selection index is the quotient of relative usage and relative availability of the respective land cover type for an individual. Red lines indicate the prediction of the GAMM with the individual roe deer as random effect. Shade represents the estimate of the 95% confidence interval. (Be aware of different scaling of the y-axes in the last row.) Estimated degrees of freedom (edf) and p-values based on F-statistics provide a rough guide to significance of the smoother: the higher the edf the stronger the smoother differs from a straight line.

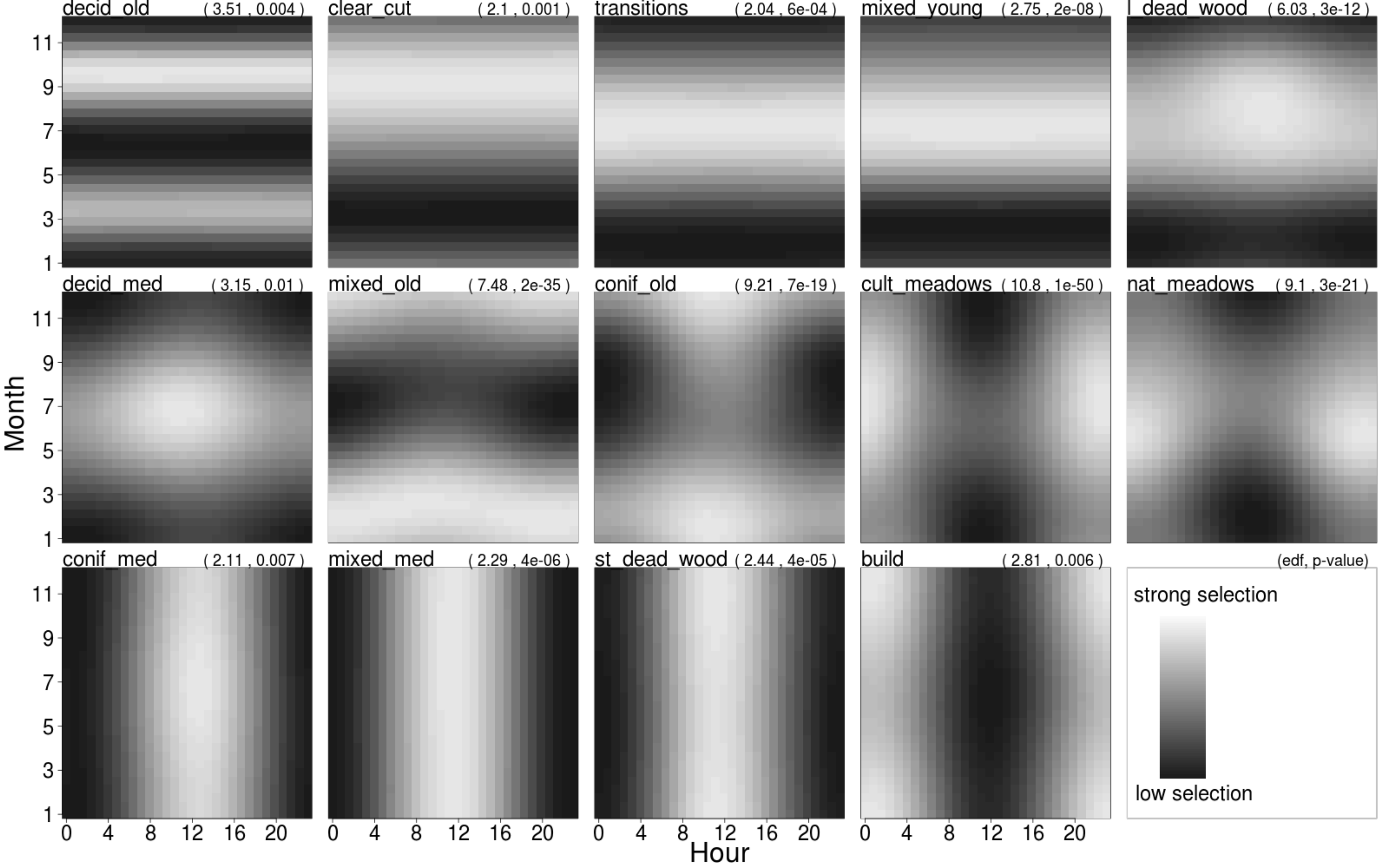

Fig.S3. Relative variation of selection strength over time of the day (x-axis) and the year (y-axis). Grey shading indicates the relative selection for the respective land cover type and can not be compared among the different land-cover types. For the absolute selection value see Figs. S1 and S2. The usage of land-cover types in the top row varied mainly over the time of the year ; diurnal usage was mostly constant. The usage of land cover types shown in the bottom row varied only over the diurnal scale. The usage of land cover types shown in the middle row varied over both, diurnal and annual scales. Estimated degrees of freedom (edf) and p-values based on F-statistics provide a rough guide to significance of the smoother: The higher the edf the stronger the smoother differs from a flat surface.

Anlage 5:

LiDAR remote sensing and GPS-telemetry data: Gaining precision in winter habitat selection of European roe deer.

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Abstract

Understanding animal movement behaviour is a key to understand the ecology of animals. How and why they use specific resources has direct implication on forest management. As movement decisions of animals take place on a small spatial scale detailed information about landscape properties are necessary to analyse GPS-based location data. The advance of remote sensing techniques facilitate the utilization of wide area high resolution data of environmental covariates. However these are rarely used in habitat selection studies.

In this study we analysed the winter habitat selection of roe deer (*Capreolus capreolus*) using estimates of vegetation cover in three different height strata, derived from high resolution airborne LiDAR. We used activity data, recorded by acceleration sensors integrated in the animal's neck collars, to differentiate between active and resting animals. We tested for the influence of temperature, snow height and wind speed on site selection. Site selection was analysed using mixed effects conditional logistic regression models in a case-control design.

Our results show that site selection was influenced by temperature, snow height, and activity status of the animals. Roe deer tended to use forests characterized by high canopy cover more frequently with decreasing temperature, and when snow height exceeded 60 cm. Active animals preferred lower canopy cover, but higher understory cover, than resting ones. High resolution LiDAR data allowed to quantify behavioural differences in dependence of weather and activity status, demonstrating that LiDAR is a promising tool for habitat studies in ungulates. Furthermore, this study underlines the importance of integrating behavioural data into habitat selection studies.

Introduction

Understanding a species' habitat selection is a major prerequisite for wildlife management concerning conservation issues on the one and forest management on the other hand. Roe deer is known to influence tree regeneration to a great extent in particular in areas where their natural enemies are missing [1,2]. This effect gains importance in wintertime where coniferous trees become a main food source [3]. The European roe deer is a medium sized ungulate that is distributed throughout Europe and adapted to wide variety of landscape types [4], with a preference for wooded habitats [5]. Roe deer are selective feeders that browse on large number of plant species [6,3]. In northern latitudes and parts of continental Europe animals have to face extreme winter conditions, that strongly influences roe deer survival [7,8]. Winter is in general a time of food shortage, both in quantity and quality and animals lose a lot of energy to compensate the thermal loss, due to low temperatures or wind chill. Additionally, deep snow may restrict moving abilities and amplifies the energy demand, especially when snow cover exceeds a height of 50 cm [9].

Resource selection functions (RSF) have been the most popular tool to link spatial patterns of animals to landscape characteristics [10–12]. The relative usage of resources is statistically compared with the relative availability by applying a form of a logistic regression. The fit of such analysis provides a quantification of the strength of resource selection. An appealing aspect of RSFs is the usage of continuous variables, abandoning a more or less arbitrary discretization of the landscape to habitat classes [13]. Habitat selection can be analysed at a very fine spatio-temporal resolution using GPS telemetry, which provides location data of cryptic organisms on almost continuous scale and thus is improving the statistical power of the analysis [14]. Indeed, in most studies the environmental covariates used to analyse site selection are not able to resolve site selection at the same spatial resolution than the positioning data does [15].

Environmental data provided from high resolution remote sensing may fill this gap [16]. Furthermore, it remains difficult to integrate behavioural observations of the animals in habitat selection studies when using huge amounts of animal locations [15]. But knowing the behavioural mode of an animal is a prerequisite to better understand an animals' habitat use [14]. For this purpose information on animal behaviour derived from bio-sensors is very promising [16]. To the authors' knowledge there are no studies available that combine a RSF-approach with behavioural observations of animals on a huge spatial scale.

In this study we aimed to integrate high resolution remote sensing data and behavioural data in a study of site selection using GPS telemetry data and a resource selection function approach. For this purpose we used data on vegetation structure derived from airborne Laserscanning (LiDAR, Light detection and ranging) and data on the animals' activity derived from acceleration sensors integrated in the the animal's neck collars. LiDAR is an established remote sensing technique which provides accurate, high resolution data for the assessment of three-dimensional vegetation structure over large areas [17]. Besides many applications relevant for forest management [18] airborne LiDAR is increasingly used in wildlife-habitat studies [19–21]. Although Coops et al. [22] underlined the utility of airborne LiDAR to map potential winter habitat of mule deer *(Odocoileus hemionus)*, no study exists that utilised this technique to analyse movement behaviour of larger forest mammals. Acceleration sensors integrated in modern GPS collars are a promising tool for the inclusion of behavioural data into wildlife habitat studies of ungulates. These sensors are able to quantify activity intensity in short time intervals, and thus deliver information on the activity status of the animals, i.e. if they are active or resting, on a quasi continuous basis [23]. This technique has been shown to be able to distinguish between locomotion, foraging, and resting for roe deer and red deer (*Cervus elaphus)* [23,24]. Here we utilize this technique to investigate differential habitat selection between active and resting animals.

We used GPS telemetry data of 15 individuals, and analysed site selection dependent on LiDAR derived estimations of vegetation cover in different height strata, using step selection functions (SSF) to sample control locations based on observed locations, and a resource-independent movement kernel [25]. Additionally we tested the influence of the animal's activity status and local weather conditions on roe deer winter habitat selection. Specifically our study aimed at testing three predictions for the winter habitat selection of roe deer in a mountain area with harsh weather conditions. We expected that in winter: (1) Roe deer generally prefer semi open habitats with high hiding cover, providing both, enough food and shelter from potential predators. Roe deer avoid open habitats in winter, where there is neither food nor cover. (2) When local weather conditions (temperature, snow height) become severe roe deer preferentially select sites with high canopy cover due to lower heat emission and lower snow level. (3) Sites used for resting are characterized by higher canopy cover than sites visited by active roe deer due to higher thermal cover.

Material and methods

Study area

Study area is the Bavarian Forest National Park (Fig. 1), which is situated in southeastern Germany along the border to Czech Republic (49◦ 3’19”N, 13◦ 12’9”E), and covers an area of 24369 hectares. Elevation ranges from 600 to 1453 m above sea level (a.s.l.). The vegetation is characterized by three major forest types. High altitudes are dominated by Norway spruce (*Picea abies*) forests, the slopes in medium elevations are dominated by mixed montane forests, mainly consisting of beech (*Fagus sylvatica*), fir (*Abies alba*) and Norway spruce, and depressions in low altitudes are dominated by alluvial spruce forests, mainly consisting of Norway spruce and birches (*Betula pendula* and *Betula pubescens*). Mean annual temperature ranges from 2 to 7.3 °C and annual precipitation from 830 to 2280 mm between valley bottoms and mountain tops. Snow cover lasts on average 139 days per year in medium altitudes with on average 50 days per year with snow depth higher than 50 cm [26]. Roe deer use the whole area of the national park in summer. In winter, they move to lower altitudes, where snow is less deep, and some individuals use the adjacent areas of the national park where they can find artificial feeding places on private hunting grounds. Within the national park area, artificial feeding places are available in and around traps, which are used to catch individuals. Food mainly consists of apple pomace, occasionally also maize and silage, and is provided daily to keep animals close to the traps. Hunting is prohibited within the national park. As a predator of roe deer, the Eurasian lynx (*Lynx lynx*) occurs in the national park [27].

Telemetry data

Roe deer were caught using wooden box traps. For measurements of morphology and body mass, trapped individuals were held at their feed. After fitting of GPS-collars animals were quickly released. GPS Telemetry data was recorded using GPS-GSM collars with integrated activity sensors (series 3.000 from VECTRONIC Aerospace, Berlin, Germany). Locations of roe deer were recorded with different time intervals, mainly ranging from 15 minutes to two hours between successive fixes. Individual animals were tracked for time periods ranging from 56 days to six month during the wintertime. Data from fawns and individuals with more than 10% missing positions due to GPS-errors were excluded from the analysis. For the remaining data, we deleted records with missing positions and removed recordings if velocities between successive locations exceeded 6.5 m/s. In order to get an equally spaced time series of roe deer locations, we only retained GPS-fixes with a time interval of 4 h. We assured independence of locations between individuals by checking movement trajectories visually. Furthermore, we only retained locations recorded in the leaf off period beginning in November until the end of April. This resulted in 1399 locations of 7 adult females 6 adult males recorded between April 2007 and December 2010 for the analysis. GPS-collars were equipped with activity sensors, which are able to capture the animals' locomotion by measuring acceleration in forward/backward and sideward motion. Acceleration is measured 6-8 times a second and averaged over a fixed time period, in this case over 5 minutes. Values were recorded on linear scale between 0 and 255. In order to identify the activity status of individuals we used threshold levels that were determined in a separate study [24], conducted in the same study area. Individuals were considered as active when the sum of both acceleration values (forward/backward and sideward) was greater than 4, and as resting otherwise.

Weather data

We used temperature and wind speed data from three weather stations Taferlruck (769 m a.s.l), Waldhäuser (940 m a.s.l.) and Waldschmidthaus (1356 m a.s.l.) (see Fig. 1) recorded in 10 min time interval, and daily recorded snow height data from Waldhäuser weather station. Temperature and wind speed values for each roe deer position were taken from the nearest weather station. In order to exclude effects of daytime on habitat selection we calculated a generalized additive model (GAM) with temperature as response, and hour of the day as predictor and used the residuals for further analysis. This way we received a variable representing the deviation from mean temperature at the corresponding daytime a GPS-fix was recorded.

LiDAR data acquisition

LiDAR data was recorded within a large area framework of the “Bavarian State Office for Land Survey and Geo-information”. Data of the study area was acquired in leaf-off period between April 2008 and November 2009 using an airborne Riegl LMS-Q 560 (RIEGL Inc., Horn, Austria) system. The system operated with a wavelength of 1550 nm, and recorded first and last return points with a vertical error of +/-0.16 m. Flight height was between 1194 and 2306 m a.s.l. (average height above ground: 776 m), and average flight velocity was 55 m/s. This resulted in a mean swath width of 832 m, a footprint with mean diameter of 38.8 cm, and an average point density of 9.8 points/m². Classification in ground and vegetation returns was performed using TerraScan (TerraSolid Ltd., Helsinki, Finland). A digital terrain model (DTM) in 1 m resolution was calculated with SCOP++ (inpho GmbH, Vienna, Austria) using “adaptable prediction” as interpolation method. To get the height of LiDAR returns above ground, we subtracted the height of each point from the height value of the underlying DTM. The resulting 3D point cloud, representing discrete returns of the land surface and vegetation cover, was used to calculate point statistics. This way various metrics, describing different aspects of the vegetation structure can be calculated [28]. Estimations of fractional vegetation cover, defined as the projection of the tree crowns onto the ground divided by ground surface area, in different strata can be calculated from point ratios [18]. Most applications of airborne LiDAR to derive fractional cover were focused on tree canopy cover, which can be estimated with high accuracy [29–31]. Some attention has also been paid on the estimation of understory cover in forests [32–34]. Wing et al. (2012) [35] received good results for the estimation of understory cover using high resolution small-footprint LiDAR data.

We calculated fractional vegetation cover of three different strata; understory (0.5 - 2 m above ground), midstory (2 - 10 m above ground) and overstory vegetation cover (10 – 60 m above ground). For this purpose points were aggregated into a 5 m x 5 m grid and values were calculated for each grid cell using the following formula:

$$vc_{h12} = \frac{(n_{h2} - n_{h1})}{n_{h2}} \qquad (1)$$

where vc_{h12} represents an estimate of vegetation cover between height above ground *h1* and *h2* (*h1* < *h2*), n_{h1} and n_{h2} represents the number of LiDAR return points below height *h1* and below height *h2* respectively. *h1* and *h2* represent the lower and upper height border of a stratum.

The estimation of fractional cover of vegetation directly above the ground is subject to errors, due to imprecision of the DTM. A previous study conducted in the Bavarian Forest National Park revealed a root mean square error of 0.3 m for the DTM [36]; therefore, we did not estimate fractional cover below 0.5 m.

Statistical analysis

To analyse habitat selection of roe deer, we applied a step selection function (SSF), a special form of a RSF [37]. In the case of a SSF control points are sampled based on empirical data of the monitored animals' movement behaviour. The direct spatial connection between two successive GPS-fixes is thereby denoted as a step. For each observed step control steps are generated using the empirical data on step-length and turning angles between successive steps of the monitored animals. To analyse habitat preferences characteristics of observed steps from an individual are compared with that of control steps, sharing the same starting point. In this study, we compared different values of vegetation cover at the endpoint of each step. By using a conditional logistic regression model with random effects we accounted for within-individual correlation and between-individual heterogeneity. Additionally, we tested whether site selection of individuals is influenced by the proximity to the nearest artificial feeding site. Data processing and statistical analysis was carried out using R 2.14.0 [38].

For the generation of the random steps, we jointly sampled step lengths and turning angles from the distributions of observed steps lengths and angles. Step length is defined as the distance between the start and endpoint of a step and the turning angle as the angular deviation of a step's direction relative to the direction of its previous step. As step length of male roe deer was significantly longer compared to females, values were calculated separately for these two groups. The length and turning angle of the observed step, the random steps should be paired with, were excluded from sampling. Following the framework of Fortin et al. (2005) [37] we generated 25 random steps for each observed step.

LiDAR-derived vegetation cover values were extracted from raster cells within a buffer of 5 m around observed and random locations. This buffer size was selected to compensate possible imprecision in positioning of the animals. Extracted values were averaged for each location. In order to prevent multicollinearity between explanatory variables, we calculated Spearman's rank correlation coefficient considering all possible variable combinations. All correlation coefficients were smaller than 0.5 indicating low collinearity between explanatory variables.

In order to compare characteristics of selected and random locations we fitted a mixed effects conditional logistic model with vegetation cover values as explanatory variables and individuals as random effects using the coxme function in the R package coxme [39]. Four separate models were fitted, each one either considering weather variables (temperature deviation, snow height, and wind speed) or activity data, weather variables and activity data, or none of both as interaction terms (Table 1). Initial models included the main effects and second order effects of vegetation cover values as well as their two way interactions with the activity status. Models including weather conditions as co-variables additionally consisted of interaction terms between the terms described in the initial model and the three used weather variables. In order to simplify models an AIC based stepwise backward selection was performed. Models performance was compared using a Chi-squared test.

In order to determine the importance of explanatory variables in the selected models, we used a method implemented in the R package BIOMOD [40]. We compared prediction of the SSF calculated from original data with the prediction from randomized values of the explanatory variables. For this purpose, we first calculated the predicted values of the SSF with given values of the explanatory variables for each observed location. Then, we calculated predicted values of the SSF randomizing each time one of the explanatory variables. Finally, correlation between predictions based on the randomized datasets and the original data was analysed. The smaller the correlation coefficient is, the higher is the independent influence of the permuted variable. From correlation coefficients, we calculated the relative importance for each variable.

Results

Male roe deer moved significantly longer distances (Wilcoxon test, $p < 0.001$, mean: 208 m in 4 h) than females (171 m). Mean snow height for all GPS fixes used in the analysis was 26.3 cm. Maximum snow height was 105 cm recorded in February 2010. Mean temperatures during the study period ranged from –4.7 °C in the night to 1.3 °C at noon. Mean observed wind speed was 1.5 m/s. Individuals stayed in average distances of 250 m to 1.2 km away from nearest artificial feeding site.

Habitat selection of roe deer

Integration of weather conditions as well as including the activity status of the animals improved tested models on habitat selection of roe deer (see Table 1). Model 1 containing interactions of weather conditions and activity status performed best (AIC: 9346), followed by the models 2 and 3 only considering weather conditions (9362) or activity status (9394) as interactions. All following results refer to the model 1 including weather variables and activity status of the animals.

Activity status of roe deer influenced habitat selection patterns (Table 2). Generally, sites selected by active roe deer were characterized by lower canopy (overstory and midstory) cover and higher understory cover than sites selected for resting (Fig. 2, 3, and 4).

While temperature and snow height had influence on preference for over- and midstory cover (see Table 2) we found no influence of wind speed on roe deer habitat selection. Roe deer preferred higher over- and midstory cover when temperature decreased (see Fig. 2). When temperatures rose more than 5 °C above average daytime temperatures animals preferred more open habitats characterized by low to medium over- and midstory cover (see Fig. 2). With increasing snow height roe deer also preferred increasing midstory cover (Fig. 3). Additionally animals strongly selected sites characterized by high values of overstory cover when snow height exceeded 60 cm (see Fig. 3).

Distance to the nearest artificial feeding place was the most influencing variable describing habitat selection of roe deer (relative importance: 0.53). The most influencing cover value was overstory cover (relative importance: 0.104) followed by midstory cover (0.088) and understory cover (0.031). Comparison of used weather variables and activity data revealed that activity status was the most influencing variable (relative importance: 0.098), followed by temperature (0.09) and snow height (0.062).

Discussion

Our analysis showed, that winter habitat selection of roe deer strongly depends on the activity status of the animal and weather conditions. This indicates that a general examination of winter habitat selection without consideration of activity status and weather conditions does not reflect all facets of roe deer behaviour. We could show some general habitat selection patterns. Roe deer either tended to use sites characterized by at least some degree of canopy cover, or sites characterized by high understory cover (Fig. 5). Thus, we can assume that roe deer avoid open sites in areas with harsh winter conditions. Roe deer primarily use open areas to forage and under described conditions we expect no food being available there. Ratikainen et al. (2007) [41] also found roe deer avoiding open habitats in winter.

We found that animals preferred higher canopy cover when it was cold compared to average temperatures or when snow heights of our reference weather station exceeded 60 cm. This result is consistent with previous studies on ungulates in general [42–45], and roe deer in particular [46,47] which also observed preference for higher canopy cover at low temperatures and deep snow. It confirms our expectations that roe deer use forests with high canopy cover as thermal shelter when temperatures are low.

We found no effect of wind speed on roe deer winter habitat selection. In a previous study increased use of dense canopy cover has been observed with increasing wind speed for roe deer [48]. The weak response in our study is probably due to a lack of information in the used weather data. Most of observed wind speeds, at the time of GPS-fixes, were below 5 m/s, so that we cannot get satisfactory results on behaviour at extreme conditions. Additionally, wind exposure strongly depends on terrain and thus can locally differ considerably from values measured at weather stations.

Overall, roe deer tended to use sites with lower canopy cover when active. This is concordant to the result of Ratikainen et al. (2007) [48], who observed that bed-sites were characterized by higher canopy cover than foraging sites. This suggests that especially resting individuals utilize the thermal cover of dense canopies. Additionally, we found roe deer preferring dense understory when active, and low understory cover when resting. The high preference of resting animals for forests, characterized by little undergrowth is reasonable to avoid encounters by potential predators. Especially lynx are dependent on the presence of understory vegetation to stalk their prey [49]. On the other hand, active bouts of roe deer in winter are mainly used for foraging [50]. Therefore, it is a reasonable result that individuals prefer sites characterized by higher understory cover, also indicating higher winter food supply, when active. Overall our results underline the findings of Mysterud et al. (1999) [47], who could show that roe deer in winter particularly have to face a trade-off between food availability and thermal cover. However, our study shows that this finding should be extended by the trade-off between food availability and protection from lynx, which animals also have to face.

Distance to the nearest artificial feeding place was the most important variable explaining winter movement behaviour of adult roe deer. This result is concordant to a study of Guillet et al. (1996) [51], who observed that roe deer tended to concentrate around artificial feeding places at extreme weather conditions in winter. This is not surprising as roe deer only store small fat reserves and individuals have to cover most of their energy by permanent food intake [9]. Our finding underlines that low food availability is one of the major challenges roe deer have to face under harsh winter conditions. However, average distances in our study were fairly high compared to that observed by Guillet et al. (1996) [51]. Although most of the animals showed up in close proximity to these places at least once, animals stayed in quite a distance for most of the time. This finding can be explained by the small amounts of food which is supplied only for the purpose of getting roe deer used to the traps. This kind of food supply cannot be compared to a full winter feeding.

Of the used LiDAR-variables overstory cover was the most important variable, but did not differ strongly from midstory cover. Since roe deer showed no basic differences in usage of over- and midstory cover, we can assume that primarily the functional characteristics of these layers, such as reduced heat emission and snow interception, are important for the animals. In contrast, we found only little influence of understory cover. This result is in line with the findings by Torres et al. (2011) [52], who analysed winter habitat selection in Norway, and found no influence of shrub cover on habitat selection. In the Bavarian Forest National Park the small influence may be explained by the presence of lynx. In this case high understory cover serves as potential winter forage source, but on the other hand enhances the risk of being killed.

In addition the difference of importance between over- and understory could be influenced by the estimation accuracies. Using LiDAR with similar footprint and point density like in this study tree canopy cover can be estimated more accurately than understory cover [29,35].

Conclusion

In this study we aimed at integrate high resolution remote sensing data and behaviourial data in a study of site selection using GPS-telemetry combined with a resource selection function approach. We could show that habitat selection of roe deer under rough winter conditions cannot be generalized, but is strongly dependent on external influences, like weather, and on the activity status of the animal. Thus our study underlines the importance of animal behavioural data in habitat use studies. We strongly recommend the integration of activity data in habitat studies of ungulates, as this holds high potential to explain variability in habitat preferences. Moreover, results show that roe deer in winter are dependent on heterogeneous habitats. These should comprise forest regeneration with high understory cover, which particularly at high snow provide potential forage for roe deer, and older forest stands with dense canopy cover, which potentially mitigates the effect of cold temperatures and high snow.

High resolution LiDAR data were well suited to depict habitat preferences in general, and particularly dependencies of site selection on activity status and weather variables. This underlines the importance of physical forest structure for site selection of roe deer and suggests the increased application of LiDAR technology in wildlife-habitat studies of ungulates. Particularly, the use of continuous and area-wide available environmental covariates allows generating detailed prediction maps on a species habitat use, that can easily be extrapolated beyond the borders of the study area and are helpful concerning forest conservation or wildlife management issues. Furthermore results can be easily incorporated in individual based models for analysing movement behaviour of animals. Thus we highly recommend the use of high resolution remote sensing data and behavioural data in habitat use studies.

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Conflict of Interest

The authors declare no conflict of interest.

Table 1 Summary of calculated mixed conditional logistic regression models explaining habiat selection and associated AIC values. Model 1 incorporates weather variables and activity status, model 2 only weather variables, model 3 only activity status and model 4 neither of the two. All models incorporated individuals as random effect. Dist_to_f: Distance to nearest artificial feeding place, OC: Overstory cover, MC: Midstory cover, UC: Understory cover, temp: deviation from mean temperature at corresponding daytime, act: Activity status of roe deer, snow: Snow height, wind: Wind speed.

Model	Included Variables	Fixed effects	AIC
1	LiDAR + activity + weather	OC + UC + MC + Dist_to_f + OC^2 + MC^2 + OC:act + UC:act + MC^2:act + MC:temp + OC^2:temp + OC:snow + MC:snow + OC^2:snow	9346
2	LiDAR + weather	OC + UC + MC + Dist_to_f + OC^2 + MC^2 + UC:temp + MC:temp + OC^2:temp + OC:snow + MC:snow + OC^2:snow + MC^2:snow + UC:wind + MC:wind + MC^2:wind	9362
3	LiDAR + activity	Dist_to_f + OC + MC + UC + OC^2 + OC^2:act +MC:act + UC:act	9394
4	LIDAR	OC + MC + dist_to_f + OC^2	9421

Table 2: Results of mixed conditional logistic regression with individuals as random effect (Model 1). Bold values indicate significant effects ($p < 0.005$) of model terms. Dist_to_f: Distance to nearest artificial feeding place, OC: Overstory cover, MC: Midstory Cover, UC: Understory Cover, temp: deviation from mean temperature at corresponding daytime, act: Activity status of roe deer, snow: Snow height.

Variable	Coef.	SE	Z	P
Dist_to_f	-0.002	<0.001	-4.54	**<0.001**
OC	2.721	0.544	5.000	**<0.001**
MC	1.341	0.547	2.45	**0.014**
UC	-1.216	0.531	-2.29	**0.022**
OC^2	-2.902	0.584	-4.97	**<0.001**
MC^2	-1.805	0.789	-2.29	**0.022**
OC:act	-0.764	0.204	-3.74	**<0.001**
UC:act	1.812	0.717	2.53	**0.011**
MC:act	-0.911	0.385	-2.36	**0.018**
OC^2:temp	-0.092	0.024	-3.81	**<0.001**
MC:temp	-0.088	0.039	-2.25	**0.024**
OC:snow	-0.038	0.014	-2.68	**0.008**
MC:snow	0.030	0.007	4.27	**<0.001**
OC^2:snow	0.052	0.015	3.37	**<0.001**

Fig. 1: Study area and its location in Germany. The black frame marks the outline of the Bavarian Forest National Park. GPS-fixes of roe deer used in the analysis are displayed as black circles, locations of weather stations as squares. T: Taferlrück, WH: Waldhäuser, WSH: Waldschmidthaus

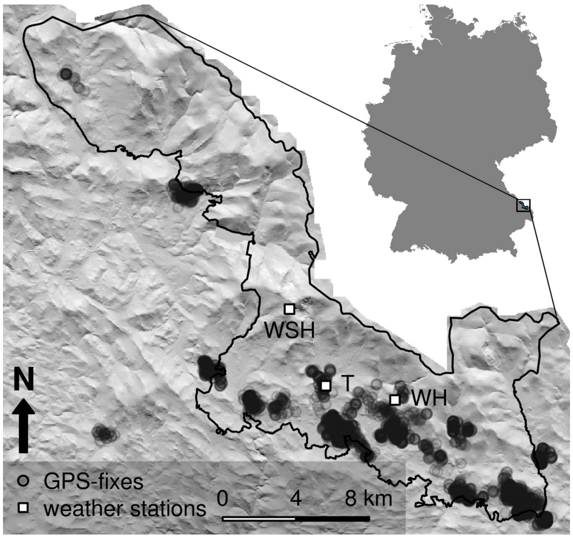


Fig 2: Predicted preference values for overstory Cover (2-10 m) and midstory Cover (10-60 m) as a function of temperature deviation from mean temperature values at given daytime for active and resting roe deer. Values represent expected values estimated by mixed conditional logistic regression; not-displayed variables were set to their data set mean. Preference values were scaled between 0 and 1 to keep results between different temperatures comparable.

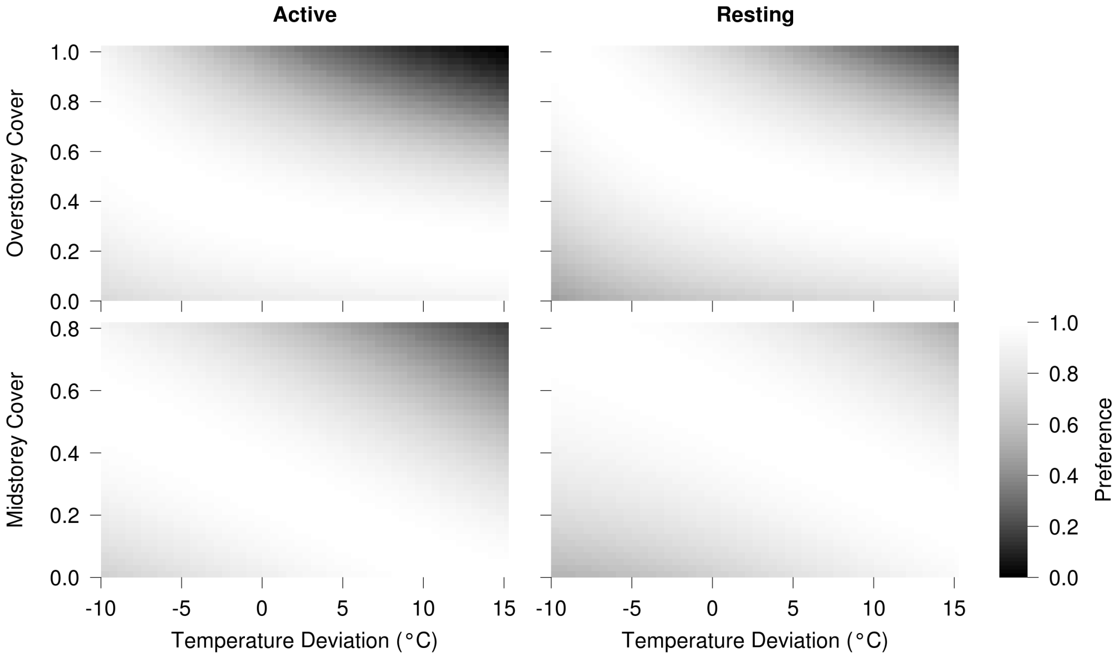


Fig 3: Predicted preference values for overstory cover (10-60 m) and midstory cover (2-10 m) as a function of snow height for active and resting roe deer. Values represent expected values estimated by mixed conditional logistic regression; not-displayed variables were set to their data set mean. Preference values were scaled between 0 and 1 to keep results between different temperatures comparable.

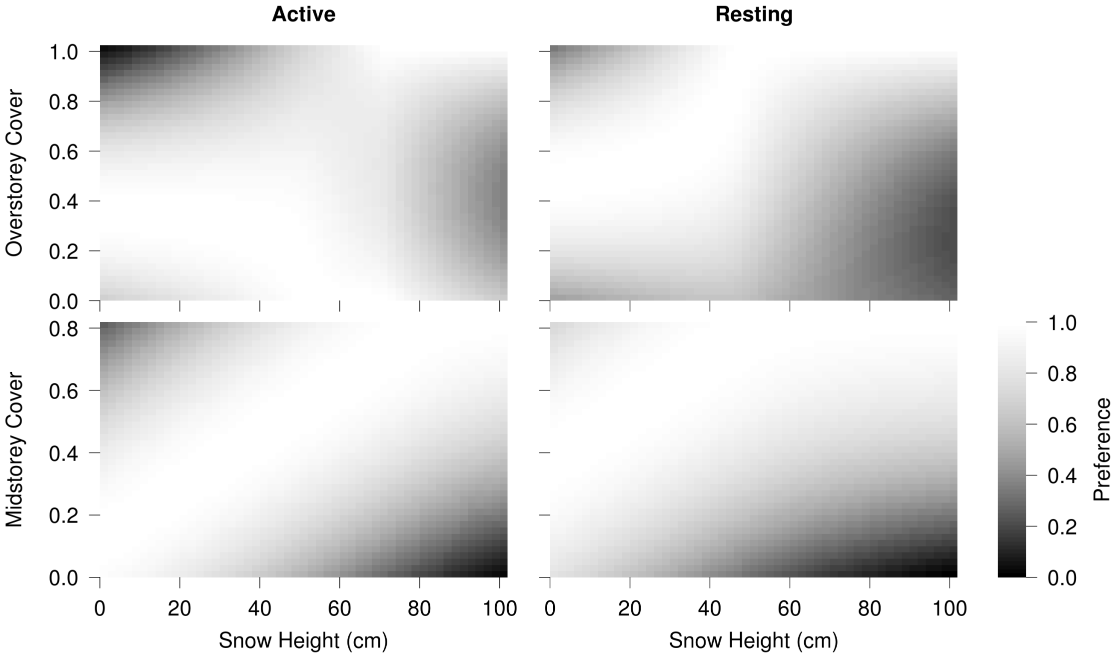


Fig 4: Predicted preference values for understory cover for active and resting roe deer. Values represent expected values estimated by mixed conditional logistic regression; not-displayed variables were set to their data set mean.

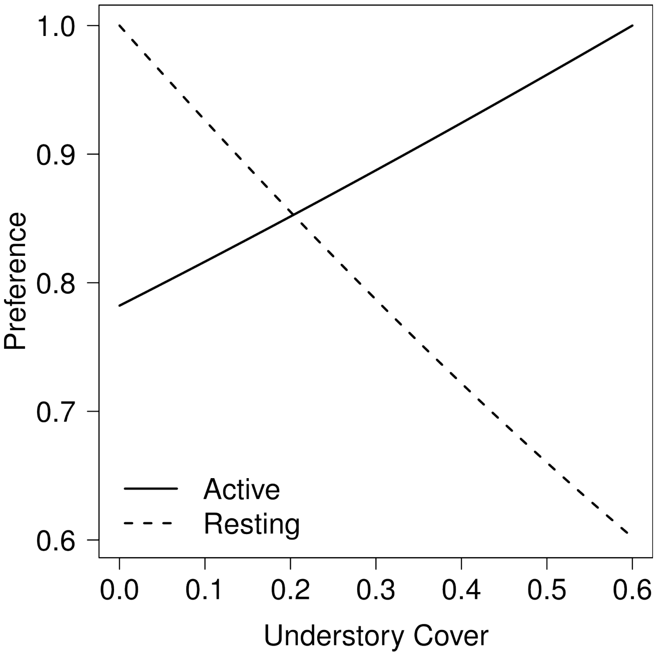
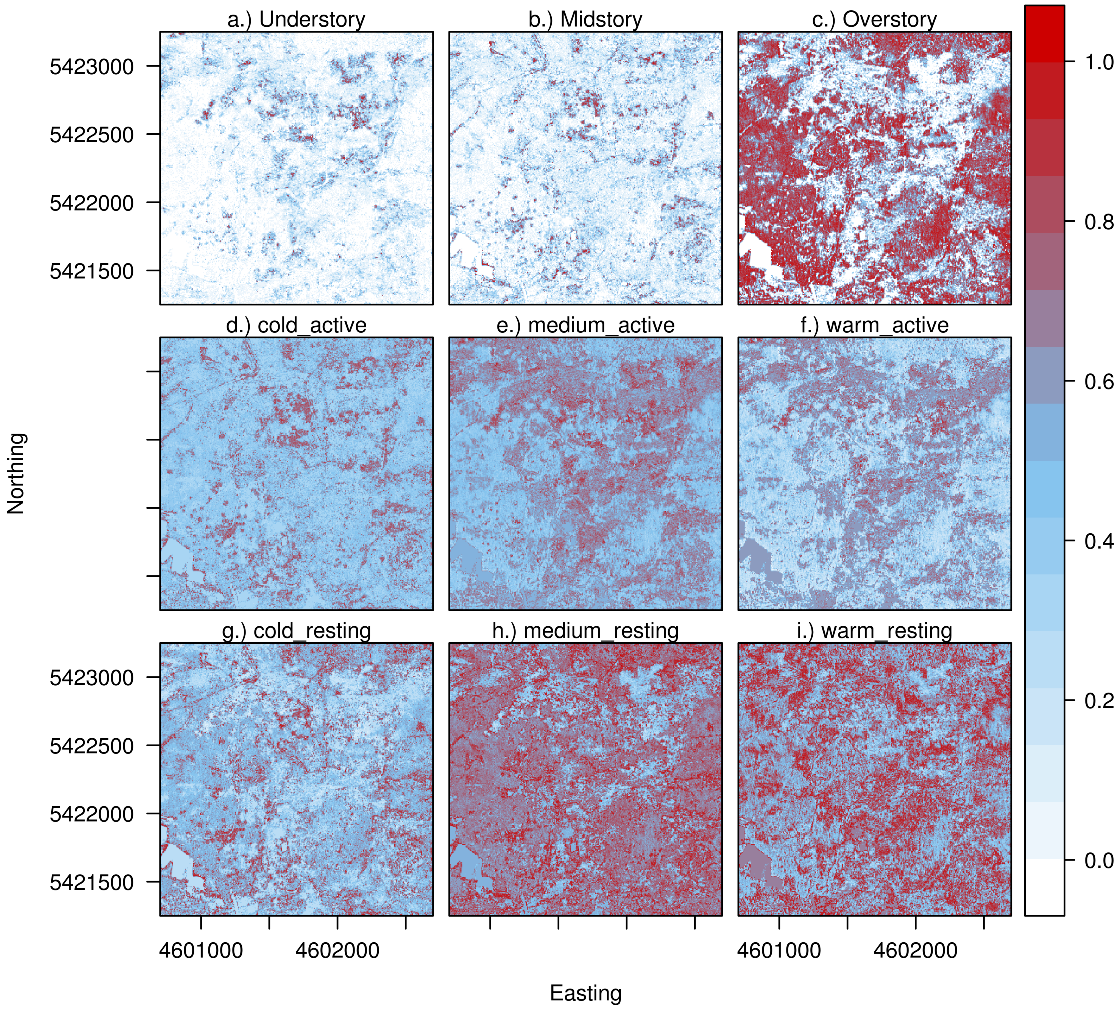


Fig. 5: Map sections of LiDAR-derived vegetation cover values (a. - c.) and predicted maps of habitat preference of roe deer for different weather condition and activity status scenarios. (d. - i.). The prediction maps where calculated using model 1, keeping the distance to the nearest feeding place constant at the dataset mean. a.) Understory: Understory cover, b.) Midstory: Midstory Cover, c.) Overstory: Overstory cover, d.) cold_active: Prediction for active roe deer at temperatures kept constant at the 10th percentile and snow height kept constant at the 90th percentile of observed values. active, e.) medium_active: Active roe deer, median temperatures and snow height, f.) warm_active: Active roe deer, 90th percentile temperature value, no snow, g.) cold_resting: Resting roe deer, 10th percentile temperature value, 90th percentile snow height value, h.) Resting roe deer, median temperatures and snow height, i.) Resting roe deer, 90th percentile temperature value, no snow.



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Anlage 6:

Seasonal variation in circadian activity patterns in red deer (*Cervus elaphus*) in Bavarian Forest National Park

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Introduction

Behaviour is a fast and important mechanism for an animal to interact with its environment. Thus, studying behaviour is a good tool to understand the ecology of an animal. In contrast to laboratory studies those usually explore single effects, investigations of the behaviour on wild animals in their natural environments (and thus in their ecological contexts) are particularly important because they reflect the entire real complexity of the ecology of the animals. However, behavioural studies on free-ranging wild animals are difficult and time-consuming due to both the shy and secretive lifestyle of the animals and the field conditions hardly to examine.

In recent years, new telemetry technologies have become available in wildlife research and collar integrated acceleration sensors are increasingly used also on free-ranging wild animals to continuously and long-term register the general activity (Ropert-Coudert and Wilson 2005; Bograd et al. 2010). General activity is controlled by endogenous pacemakers (Aschoff 1955) and related to regular physiological and behavioural patterns of a species, particularly in ruminants which depend on regular feeding rhythm (Hofmann 1989). Thereby, the circadian rhythm is the basic and common component determined by the endogenously central nervous peacemaker system in the Nuleus suprachiasmaticus (Gerkema et al. 1990; Refinetti 2000; Hirota and Fukada 2004; Perreau-Lenz et al. 2004; Weinert 2005), but being also susceptive to outside synchronisation (Yerushalmi and Green 2009). One of the most effective and reliable signals in entraining circadian rhythms is the light-dark cycle (van Oort et al. 2007; Scheibe et al. 2009). Further on, expression of the behavioural 24-h rhythm depends on additional external factors like temperature, food availability, or predation pressure which can modify phase and amplitude of the peripheral processes (masking, Munoz-Delgado et al. 2004) by optimising activity budgets (Loe et al. 2007). Finally, the general activity of an animal base in a daily pattern which is altered by season to react on seasonal changes in environmental conditions (Scheibe et al. 2001) in order to balancing individual energy reserves (Pépin et al. 2006) and to maximize the benefits animals can derive from limited natural resources. The interaction between entrained internal rhythms of naturally different phases and secondary masking effects seems to be responsible for intra- and inter-individual variability of patterns of daily rhythms; a wide intra-species gradient of temporal niches is seldom investigated, especially in larger mammals (Remmert 1969; Mrosovsky 1999; Refinetti 2006).

Activity patterns of deer have been studied in several species during the last decades, e.g. roe deer (*Capreolus capreolus*) (Cederlund 1981; 1989; Schober and Wagner 1995, Krop-Benesch et al. 2012; Pagon et al. 2013), rocky mountain elk (*Cervus elaphus*) (Green and Bear 1990), white-tailed deer (*Odocoileus virginianus)* (Kammermayer and Marchinton 1977; Beier and McCullough 1990; Coulombe et al. 2006) and moose (*Alces alces*) (Cederlund 1989). Activity data on free-ranging red deer covering a complete seasonal cycle were obtained by Georgii and Schröder 1978, Georgii 1981 and Kamler et al. 2007 using variations in radio-telemetry signals derived from the (moving) angle of the animal's head and discriminating between an active and inactive state. Although these data allow valuable insights into the daily and seasonal activity patterns of a species, they do not allow a thorough analysis of circadian rhythmicity specially its seasonal changes, Cosinor, and Fourier analysis. This requires continuous time-series with short sampling intervals over several months (Sinz 1978). Differently to previous studies of activity patterns on red deer, our study investigated the year-round total activity levels of red deer under relatively natural conditions. Using accelerometer within GPS-collars, we measured activity in red deer for up to 22 months continuously to gain information on activity levels and structure of daily and seasonal activity in six male and six female red deer in the National Park Bavarian Forest. We discuss whether the seasonal changes in activity can be explained as response to habitat changes (availability of browse) during the vegetation period. In regard to this, we expect higher activity levels and more activity bouts in summer than in winter. Additional hypotheses were that activity of red deer would exhibit bimodal crepuscular peaks, and that sexual and seasonal differences in activity would occur based on several activity parameters (i.e., daily mean activity, daily mean number and duration of activity bouts).

More specifically, our assumptions were as follows:

1. Red deer were expected to adjust their daily activity pattern to outside light-dark cycle, like was reported for other ungulates. If so, the pattern should also change seasonally, accordingly to annual changes in light-dark cycle. Anthropogenic management of red deer in Bavarian Forest National Park (winter enclosures) leads to suddenly and significant changes in activity pattern; we expect a lower activity level and a reduced number and duration of daily activity bursts.

2. As animals chose their sheltering and resting places in order to experience more favourable temperature regimes and reduce heat loss (Arnold et al. 2003) or not risk overheating (Maloney et al. 2005) thermoregulation aspects would most likely disguise the effect of seasonal photoperiod on the animals’ activity, with a reduction of activity during hottest and coldest hours in summer and winter, respectively.

3. Due to the strong sexual dimorphism in red deer with males considerably larger than females, differences in activity patterns between sexes might also be expected. However, the annual biological cycle of the species most likely dictates differences between sexes, at least during the reproductive and/or territorial period. Accordingly, we expect differences in activity patterns between sexes, presumably with an increase of adult male activity during the rut in autumn.

4. Apart from the winter enclosures, red deer in Bavarian Forest National Park lives under relatively natural and undisturbed conditions: As natural predator only Eurasian lynx (*Lynx lynx*) occurs with roe deer (*Capreolus capreolus*) as its main prey in Bavarian Forest National Park. Human hunting is prohibited and the core of the National Park contains a strict nature reserve, where human activities are strictly controlled and limited. As ungulate prey species are supposed to reduce their activity during high predation risk or shift their activity to nocturnal (Lima, 1998), we predict that red deer in the National Park is rather active during day than during night since there is no higher risk by human hunters and predators.

Material and methods

Study area

The Bavarian Forest National Park covers an area of 244 km² in South-Eastern Germany along the border with the Czech Republic (49° 3' 19" N, 13° 12' 9"E). Together with the adjacent Bohemian Forest, the area comprises one of the largest contiguous forested areas in central Europe, the Bohemian Forest Ecosystem. The study area comprised the Rachel – Lusen region, a section of 130 km² of the Bavarian Forest National Park. The area is mountainous with elevation varying between 600 and 1,453 m. Climate data on measures of temperature and snow cover are provided in Table 1.

There are three major forest types within the National Park. Above 1,100 m (16 % of the area) there are sub-alpine spruce forests with Norway spruce (*Picea abies)* and some mountain ash (*Sorbus aucuparia)*. On the slopes, between 600 m and 1,100 m altitude, there were mixed montane forests with Norway spruce, white fir (*Abies alba),* European beech (*Fagus sylvatica)* and sycamore maple (*Acer pseudoplatanus*) (68 % of the area). In wet depressions (16 % of the area), often associated with cold air pockets, in the bottom of valleys there were spruce forests with norway spruce, mountain ash, and birch (*Betula pendula*, *Betula pubescens)* (Heurich and Neufanger 2005). Since the mid 1990s, the forests of the National Park were affected by massive proliferation of the spruce bark beetle *Ips typographus*. By 2006, this had resulted in the death of mature spruce stands over an area amounting to 4,430 ha (Lausch et al. 2010).

Table 1: Climate data from the weather station Waldhäuser at the Bavarian Forest National Park for 2003 and 2008. Median max and min temperature is calculated from the daily extremes, absolute max and min temperature is the highest respective lowest value measured within this month during the entire study.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Temp max [°C]	10.3	13.1	16.9	23.9	28.3	28.2	31.9	31.5	26.4	22.0	19.9	14.8
Median temp max [°C]	0.2	0.7	4.3	11.5	15.3	19.9	21.0	19.5	16.2	12.3	4.5	1.7
Median temp min [°C]	-3.7	-5.1	-2.4	2.2	5.8	10.7	11.2	10.4	7.6	3.9	-1.1	-3.0
Temp min [°C]	3.9	4.3	6.0	10.7	17.2	16.2	18.8	18.9	15.9	11.7	13.5	6.0
Mean snowfall [cm]	50.9	73.3	56.5	9.1	0.0	0.0	0.0	0.0	0.0	0.3	15.9	25.0
Mean snow cover [cm]	5.0	4.8	4.2	1.2	0.0	0.0	0.0	0.0	0.0	0.3	3.6	2.5

Wildlife Management in the National Park Bavarian Forest

The most important objective of the National Park is the protection of the undisturbed dynamics within natural communities. Accordingly, one of the principles should be to avoid regulation of the wild ungulate population through human intervention. However, some management might become necessary if certain National Park goals or the rights of adjacent private landowners suffer negative impacts, for example because of overabundance of ungulates.

Wildlife control measures are undertaken only in the management zone of the National Park. As a result, the animals in nature conservation zone of the National Park do not experience hunting pressure. The current extent of the zone that is released from control measures encompasses an area of 17,000 ha (71% of the present total area of the National Park).

During the summer, red deer in the Bavarian forest mostly remains inside the national park boundaries while, during wintertime, it moves into lower regions. These are partly located outside the park boundaries in areas with intensively managed private and state forests. In order to avert economic damages in those areas, due to browsing and bark stripping, the animals are kept within the park in so called ‘winter enclosures’. These are fenced areas of about 30–50 ha, including a central feeding site. In fall the animals are rounded up into the gates and are kept there until the vegetation has recovered (Heurich et al. 2011, Ludwig et al. 2012).

Control of the red deer populations is carried out primarily in the winter enclosures by game wardens employed by the National Park. Here, the animals are culled selectively and quickly, with regard for animal welfare, and without disturbing the other animals. The percentage of animals killed in the winter enclosures is about 50%. In the management area of the park, red deer are also hunted from high seats to limit population growth.

Trapping red deer

The animals are live captured with a facility which is designed in the shape of a corral. The animals are attracted to the corral by food (grass silage, hay, apple pomace, sugar beets). The diameter of the corral is 20 to 50 m and its height is 3.5 m. After the animals have entered the corral, the gate (approximately 3 m long) is closed with a cable winch that is operated manually from a hidden position. Afterwards, the deer are guided to a 6 m long lane that can be partitioned into two separate compartments. In addition, the lane narrows down from 1.4 m at its entrance from the corral to 1m at the exit on the opposite end. The side walls of each compartment have four hatches, 70 x 30 cm in size. These are used for marking the animals and fitting them with collars with attached GPS transmitters. This procedure does not require immobilization of the deer. When captured, red deer behave calmly and are quite docile. Even the immediate presence of humans does not disturb the animals (Heurich 2011).

Animals

Six male and six female red deer have been equipped with Vectronic radio collars. A total of 111,960 hours of data has been recorded for analysis.

Table 2: List of studied animals

Name of animal	Sex	Age when collared	Activity measurements		
			from	to	number of days
Anita	female	1	12.04.2007	14.04.2008	369
Barbara	female	15	17.04.2005	26.04.2006	374
Faballa	female	2	07.04.2006	31.01.2008	665
Hera	female	1	12.04.2007	01.04.2008	359
Oma	female	12	18.03.2003	07.04.2004	385
Susi	female	2	03.05.2004	27.10.2005	543
Christoph	male	3	07.05.2005	13.08.2006	493
Dane	male	4	10.05.2005	22.01.2006	261
Emil	male	5	12.05.2005	22.01.2006	259
Fritz	male	3	27.04.2004	17.04.2005	355
Paul	male	8	27.04.2004	08.01.2005	257
Willi	male	9	07.04.2004	18.04.2005	381

Data Recording

Activity was recorded by acceleration sensors in the collars in two channels, forward-backwards and sideways. Activity was measured six to eight times per second as true acceleration between two consecutive measurements and transformed into a relative measure covering values between 0 and 255. These data were averaged over 5-minute intervals.

Both activity channels recorded very similar measures in roe deer (Pearson correlation coefficient r = 0.95, Stache et al. 2013). The relationship between activity, behaviour of the animal, and activity values as measured by the collar was accessed in red deer (Löttker et al. 2009) and in roe deer (Heurich et al. 2011). Both studies found a significant correlation between resting, foraging, and locomotor activity and the acceleration values of the forward-backward channel but not for foraging activity and the acceleration values of the sideways-channel. Therefore, only data from the forward-backward channel were used in the current study.

Data analysis

For data analysis, we used the coordinates 49° 54’ N 13° 29’ E as the geographical centre of all trapping locations and home ranges. We obtained times of sunrise/sunset and nautical twilight (sun -12° below horizon) from the US Naval Observatory (2008) and calculated them with the computer software “Activity Pattern” (Vectronic Aerospace GmbH).

Phenological seasons were derived as mean from the begin and the end of each season as obtained from the nearest weather station (Deutscher Wetterdienst) at Straubing (48° 53’ N 12° 34’ E) for the period between 1961 and 1990. Start and end of each season is defined as follows: spring from 10 March to 01 June beginning with the onset of hazel (*Corylus avellana*) bloom, summer from 02 June to 29 August beginning with the onset of black elder (*Sambucus nigra*) bloom, autumn from 30 August to 28 October beginning with the appearance of the first black elder (*Sambucus nigra*) fruits, and winter from 29 October to 09 March beginning with the onset of needling of European larch (*Larix decidua*). We defined the “reproductive period” from March to August as period between the implantation in females and beginning of antler growths and preparation for rut in males in March and the rut in August. The “vegetation period” was defined from April to October, as opposite of the harsh food conditions during winter, meaning as period in which food supply is highly available and of changing quality.

Standardisation of individual values

Acceleration of the collar can be influenced by collar circumference in relation to the circumference of the animal’s neck, by fur thickness, and differences in sensor sensitivity. Hence, the same movement might result in differing acceleration values for different individuals. Since we did not aim on absolute values, but on changes in the activity pattern, we used standardised acceleration values for form estimates, mean daily activity and day-night relations by z-transformation of the absolute raw data of each animal with the following equation:

$$z_i = \frac{x_i - \bar{x}}{s}$$

in which x is the original value, $\bar{x}$ = mean of an individual's activity, s = standard deviation of an individual's activity. For peak analysis, we used the original data, but calculated individual thresholds to define a bout.

Daily activity patterns

We plotted acceleration data of forward-backward movement with the software "Activity Pattern" (Vectronic Aerospace). Actograms give a more detailed picture of the fine-scale activity pattern of individuals than plots showing aggregated values of all animals, and are a good demonstration of either variability or constancy of pattern. We plotted monthly 24-hour patterns of activity (form estimates) for males and females. These were calculated as the mean acceleration value for a certain time of day (e.g. 15:05), then averaged over all days per month and individual and then across all individuals.

Cosinor analysis

We calculated the cosinor of the circadian periodicity for each individual according to Nelson et al. (1979) with "Activity Pattern" for four time spans of 30 days each with the summer/winter solstice and the spring/autumn equinox as central dates. Cosinor analysis uses the least squares method to fit a sine wave with fixed period length (here 24 hours) to a time series (here activity data) and calculates the acrophase (timing of the maximum of the fitted sine wave), the amplitude, and the degree of fit. The acrophase describes the centre or focus of most activity not being necessarily the maximum of activity, especially in bigeminus patterns.

Day-night relation of activity

To characterise the seasonal variations in the intensity and distribution of activity, total sum of activity per 24 hours and day-night relation of activity were calculated as monthly means across all individuals of one sex. Day:night ratio (r) was calculated as

Ratio $r = (c_d - c_n) / (c_d + c_n)$

in which c_d = mean level of activity during daytime (sunrise to sunset) and c_n = mean level of activity during night-time (sunset to sunrise).

Peak analysis (time budget)

The mean number of activity peaks per day and the mean duration of single activity peaks were calculated for each month as means across all individuals. For this purpose, data were summarised in 15 min blocks. Activity peaks consisted of blocks in which mean activity exceeded 10% of the maximum activity of the tested individual.

Frequency analysis

Autocorrelation functions were calculated for activity data of 28 continuous days of each month to eliminate single, not periodical shares (noise component).

From these calculated autocorrelation the monthly power spectra were drawn, consisting of the periodogram ordinates for all Fourier frequencies w = 2pj/n, j = 1,..., q with q = n/2 (n even) or q = n/2 - 1 (n odd), with n being the number of data points in the sample (Scheibe et al., 1999). The periodogram ordinates (which are basically variance components assigned to cyclic fluctuations containing n/j data points per cycle, j = 1,..., q) were tested for statistical significance (according to the test of R.A. Fisher in Andel, 1984) provided the significant periodic components of the original data series. For frequency analysis the self-developed Python-scripts (freely available and described under https://bitbucket.org/elpres) was used.

Statistical analysis

The number of individuals in this study is relatively small, so the power of a sex-specific comparison would be rather weak. Since we wanted to show basic species-specific patterns in activity, we chose the conservative approach of pooling both sexes. Both sexes contributed almost equally to the sample, so we did not expect significant differences where opposite sex-specific trends in relation to the expected effect are present.

For mean activity, day-night ratio, peak number, and peak duration we used means (rather than medians or other estimators of a central tendency) because the very large sample size of 5-min or 15-min intervals used to aggregate the data to calculate the means will lead to small standard errors. In addition, as long as the biases in the means of particular months of particular individuals are random with respect to the hypothesised effects, they will be of little importance for the statistical analysis.

We compared means of total daily activity, day-night ratio, peak number per day, and duration of single peaks for all individuals between months and across seasons using the ‘nonparametric marginal model’ (NMM) for repeated measurements developed for analysis of time-dependent, longitudinal data (Brunner et al. 2002). This class of nonparametric models for repeated measurements makes no assumptions on the distribution of the data, uses only the marginal empirical distributions of the data and acknowledges the dependency of repeated measurements typical for longitudinal data. The NMM is superior to well-known nonparametric statistics frequently used for repeated measures such as the Friedman test, which make rather restrictive but little known or appreciated assumptions about the structure of the variance-covariance matrix rarely fulfilled by longitudinal data in medicine, ecology or behaviour and thus are unsuitable for the analysis of the kind of longitudinal data considered here.

For small sample sizes, the NMM is also superior to general linear models which make even more restrictive assumptions than the Friedman test. Testing for significant differences between the marginal effects of different months (e.g. does the distribution of activity values significantly vary during spring between the months March, April, and May?) was performed by employing the ANOVA-type statistic (ATS) as recommended by Brunner et al. (2002) which follows an F-distribution; unlike a parametric analysis of variance, the ATS has a degree of freedom for the error term of infinity.

The NMM can also be used to calculate the relative marginal effects and their 95% confidence intervals to provide a graphical representation of effect changes between time points. A relative effect of 0.5 for a given time point (month) indicates that it is equivalent to the mean. If the effect is lower than 0.5, than the values collected for that time point tend to take on smaller values as compared to the results of all time points. The smaller the relative effect the stronger the tendency to smaller values. If the effect is larger than 0.5, then the values collected for that time point tend to take on larger values as compared to the results of all time points. The effects are termed relative marginal effects if - as in the case here – the entire distribution (and not just the means) of individual data for each month are used to check for changes in the distribution of data points between months (a more general approach than focusing on the mean or other central tendencies). In other words, the graphical illustration of relative marginal effects is equivalent to a transformation of original measurement values; relative marginal effects can therefore be used to directly compare the strength of seasonal changes amongst different parameters such as total daily activity, day-night ratio, peak number per day or duration of single peaks. For further details see Brunner et al. (2002).

Results

Actogram

In both sexes, activity was clearly organised in two seasonal patterns (Fig. 1): Between May and October, while deer was free roaming, activity was distributed throughout the complete 24 hours with pronounced maxima during twilight. Activity at night was slightly higher than during the day. In the morning, a resting period was seen in most individuals. A second, shorter resting period was visible after end of nautical dawn. In some of the males, activity increased in September. From November to April, while deer was inside the winter enclosures, activity was generally reduced, especially in the morning; the maximum of activity lied in the afternoon. Twilight maxima were still visible, but much weaker than during the free roaming months.

Daily activity patterns

These patterns are underlined by the monthly mean day patterns (Fig. 2). During free-ranging months, twilight peaks were pronounced. While a period of reduced activity was seen in the females in the morning in May, morning activity increased to mean daily level towards autumn. The pattern of activity changed in the winter enclosure. The morning peak was very weak and disappeared in some individuals. From January to April, a peak in the afternoon appeared which extended into dusk. The individual actograms (e.g. Fig.1) show, that these were actually two peaks, one in the afternoon, followed by a short period of reduced activity, and a dusk peak. The dusk peak was followed by a resting period after nautical dusk.

Cosinor analysis

All tested animals displayed a significant 24 hour periodicity in all seasons (Cosinor, $p < 0.05$, Fig. 3). Most acrophases lay in the first half of the night, but some individuals had an acrophase in the afternoon. In winter, individual differences were bigger; all tested females had acrophases during daytime, mostly in the afternoon, but in one case in the morning.

Seasonal variation of activity parameters

The mean daily level of activity showed significant differences between months, especially during the reproductive season from April to October (Fig. 4A, NMM, n=5, ATS=3.062, $df_1 = 2.190$, $df_2 = \infty$, $p < 0.05$). Activity increased during spring (March to May, NMM, n=5, ATS=10.395, $df_1 = 1.790$, $df_2 = \infty$, $p < 0.001$), decreased during summer, especially in the males (June to August, NMM, *n*=12, ATS=6.674, $df_1 = 1.200$, $df_2 = \infty$, $p < 0.01$), further decreased during autumn (September to October) after a peak (again stronger in the males) in September (NMM, *n*=12, ATS=18.014, $df_1 = 1.000$, $df_2 = \infty$, $p < 0.001$) and reached the lowest levels in winter (NMM, *n*=8, ATS=7.280, $df_1 = 1.784$, $df_2 = \infty$, $p < 0.01$).

Activity was slightly more common during night, though differences between day and night were rather small (Fig. 4B). There were no significant changes between months.

A seasonal pattern was seen in the daily number of activity peaks during the reproductive period (NMM, *n*=7, ATS=6.329, $df_1 = 2.123$, $df_2 = \infty$, $p < 0.01$), but not in their duration (NMM, *n*=7, ATS=1.436, $df_1 = 3.645$, $df_2 = \infty$, $p < 0.22$). During spring, the number of activity bouts per day increased significantly (NMM, *n*=7, ATS=4.846, $df_1 = 1.474$, $df_2 = \infty$, $p < 0.05$), as did their duration (NMM, *n*=7, ATS=3.770, $df_1 = 1.895$, $df_2 = \infty$, $p < 0.05$). Peak numbers remained high during summer and slowly decreased during autumn (NMM, *n*=12, ATS=7.404, $df_1 = 1.000$, $df_2 = \infty$, $p < 0.01$). The highest mean number of peaks per day was 7.75 in May for the females and 7.57 in August for the males. The lowest mean number of peaks per day was measured in January with 6.28 for the females and 5.75 for the males. Mean duration of activity bouts was between 18.00 min (males in April) and 25.73 min (males in June).

Frequency analysis

The plot of the monthly power spectra (Fig. 5) shows the existence of significant periods during the different months of the year to demonstrate occurrence of seasonal variation of different spectral components. It shows that the 24 hour period is a strong component of the activity rhythm during the complete year. Also strong, but almost absent in May and from July to September, is the 12 hour period. Important ultradian periods are 8 , 6, 5 and 4 hours. No distinct seasonal pattern is visible.

Discussion

Diurnal activity patterns

Diurnal activity patterns in our study clearly showed two patterns related to season and management, but there was little difference between sexes. During the free-ranging months (May to October) we observed a pattern with a mostly continuous succession of resting and activity bouts, pronounced peaks at twilight and a resting period following the morning peak. Twilight peaks are typical for red deer studies (Berger *et al.* 1998; Bubenik and Bubenikova, Jr. 1967; Georgii 1984; Georgii 1981; Georgii and Schröder 1983; Pépin *et al.* 2006) and have also been shown for rocky mountain elk (Green and Bear 1990), white-tailed deer (Beier and McCullough 1990; Coulombe *et al.* 2006; Kammermayer and Marchinton 1977), roe deer (Cederlund 1989; Krop-Benesch *et al.* 2012; Schober and Wagner 1995) and moose (Cederlund 1989).

There were two different daily patterns in the studied animals, with a very clear cut between them. This cut correlated with the moving of the animals from free-range to the winter enclosure in November and their release in April. The free-ranging animals showed alternating bouts of activity and resting during the entire day with distinct twilight peaks. Usually, there was a resting period in the morning, which disappeared during fawning in the females and during rut in some males. A second regular resting period was observed after the dusk peak. Between these peaks and resting periods, activity was quite evenly distributed.

During refinement to the winter enclosure, the activity pattern changed severely. For once, activity levels dropped visibly in all animals. The dusk peak remained, but was weaker than in the months before. The morning peak was very weak or disappeared completely. There also was little activity during the morning hours. The reason for this change in activity can be caused by two factors, (i) the man-made influence of husbandry procedures and the restricted space in the winter enclosures, and (ii) an evolutionary adaption to the harsher conditions in winter.

Arguments for the influence of husbandry procedures can easily been found. Red deer in the winter enclosures had less space to roam and less need to forage in a wide area, since they were artificially fed on a daily basis. Maintenance work and provision of fresh food is done in the morning, resulting in human presence until about 12:00. Red deer avoided the workers during this time, what most likely accounts for the reduced activity. After the workers had left, red deer approached the feeding stations, where they are fed silage and hay *ad libitium*. Therefore, foraging behaviour could be concentrated to the afternoon and would generally be reduced to a small area, resulting in less locomotor activity.

A second reason for the change in activity patterns might be the colder temperatures during winter. Low levels of activity in winter have also been reported in other studies (Arnold *et al.* 2009; Berger *et al.* 2002; Georgii 1984; Georgii 1981; Georgii and Schröder 1978) and are interpreted as an adaptation to the poor food conditions during cold temperatures and snow cover. Krop-Benesch et al. (2013) found reduced activity levels and a slight shift of activity into the daytime in roe deer in the same area.

Arnold et al. (2003) found that at low air temperatures, heart rate and subcutaneous temperature in red deer decreased and animals entered a state of temporary hypometabolism. These bouts of low body temperature have been mainly observed after midnight and coincide with the coldest parts of the night.

They suggest that circulation in red deer is reduced, particularly in the limbs, which might result in ‘numb legs’, reduced manoeuvrability and therefore reduced locomotor activity. This hypometabolism would explain two of our findings: first that nocturnal activity in winter is lower than in summer and second that the dawn peak in winter is reduced in comparison to summer and shifted towards the morning hours.

Activity in our study increased in April. Food intake has been shown to increase at this time of year (Arman *et al.* 1974; Suttie *et al.* 1983) due to the high energy requirements of antler growths, gestation and lactation. Corresponding to that, Georgii (1984) reports an increase in activity during April. This increase was stronger than in our study, but our study animals were refined by the winter enclosures, so activity could not increase to the same intent as in free-ranging red deer.

In May, winter enclosures were opened and red deer dispersed from the confined space of the enclosure into their summer home ranges, covering wider distances and thus displaying more locomotor behaviour (*unpubl. data*). Georgii (1984), too, observed this dispersion in the Bavarian Alps in April with snow melt and therefore increased manoeuvrability of red deer. High activity levels during summer can be related to fawning in May and June, and to rut in September, which is more clearly visible in the activity plots (Fig. 1) than in the monthly means (Fig. 4) due to its short duration of about two weeks.

Day-night relation of activity

In our study, red deer was slightly more active during night than during day, similar to the results of Georgii (Georgii 1984; Georgii and Schröder 1983), but there is a finer pattern undereath. Cosinor analysis shows individual acrophases between dusk and midnight at all seasons, and all animals showed distinct activity peaks during twilight, a time span which we defined as part of the night. In winter these peaks were smaller than in summer, so the day-night ratio becomes more diurnal. Also, there is relatively high activity during the winter afternoons. Based on the work of Arnold et al. (2003) it can be expected that red deer shifts its activity into the warmer daytime.

As already discussed, red deer avoided the proximity of workers in the winter enclosures. It has been discussed by other authors, whether the often observed nocturnality of red deer is a strategy to avoid hunting or contact to humans (Berger et al. 2002; Fischer 1985; Georgii and Schröder 1983; Scheibe 2009). Berger et al. (2002) and Pépin et al. (2006) reported relatively more activity during the day in captive red deer without hunting. Hunting of red deer at the core area of Bavarian Forest National Park stopped in 1986, but home ranges of males in our study included areas in which hunting is still performed. Also, red deer is subject to husbandry procedures like driving, restraining and culling at certain times during winter, so vigilance should be high, leading to avoidance of humans.

During summer, high temperatures and insects might cause deer to shift their activity into the night. Decreased activity due to insect pests have been found by Berger et al. (2002) and Pepin et al. (2006), and frequent observations by park staff have confirmed similar problems at National Park Bavarian Forest.

Activity bouts – daily pattern and its seasonal changes

Activity patterns in red deer, as typical for a ruminant, are highly influenced by feeding ecology (Hofmann 1989), and locomotor activity is linked to a high degree to feeding behaviour (Löttker et al. 2009). As an intermediate feeder, red deer chooses a mixed diet, but avoids fibre as long as possible (Hofmann 1989). In times of high availability and highly digestible food (e.g. forbs), red deer should display a high number of activity bouts due to short foraging and digesting times. The resulting high overall food intake would allow activities with high energy demands, e.g. reproduction. In winter, red deer has to rely on plants with high fibre content (e.g. coniferous trees). Food is digested slower, resulting in fewer feeding bouts and less energy intake (Hofmann 1989).

Our results for the number of bouts fit into this prediction. There were fewer bouts in winter, and their number increased in spring with fresh, highly digestible vegetation and larger home ranges. There also was an increase in the duration of the single bouts in spring, which can be explained by migration into the summer home ranges of the deer at Bavarian Forest (Heurich et al. 2007).

The seasonal changes in activity bouts seem to be inconsistent between former studies. Georgii (1981) found slightly fewer, but longer bouts in summer in free-ranging red deer in the Bavarian Alps. Pépin et al. (2006) found more, but shorter activity bouts in captive red deer in Auvergne, France, in summer. We found more and slightly longer bouts in summer then in winter. Although in all studies, red deer had supplementary feeding in winter, in our study, red deer also was refined to winter enclosures. This resulted in smaller home ranges and less necessity to forage for food. Our data show very clearly the immense impact of the winter enclosure on the deer's activity, which drops visibly at the beginning of the deer's confiment. It is therefore not surprising that the bigger home ranges are reflected in an increase in both number and duration of activity bouts.

Influence of winter enclosures

The comparison between activity patterns in summer with a natural size of home ranges and winter with its man-made restrictions suggests the need to re-think the use of winter enclosures. Unarguably a reduction of activity and food intake as adaptation to the harsher winter conditions is natural, as has been discussed by several authors (Arnold *et al.* 2009; Berger *et al.* 2002; Georgii 1984; Georgii 1981; Georgii and Schröder 1978). It has also been shown in the same area in free-ranging roe deer (Krop-Benesch et al. 2013). However, the change in activity patterns directly linked with the capture of the red deer is stronger than would be expected based on ecological conditions. There is also reason to believe that the presence of the keeper's in the morning might result in even lower activity during the day,

The seasonal pattern of high activity in summer including a peak during rut and low activity in winter was similar to other studies too (Arnold *et al.* 2003; Georgii and Schröder 1983), suggesting that this is a generic pattern in red deer. Differences have been found in the amount of change in spring and autumn, which was steeper in our study due to the refined winter enclosures. Mean daily activity, number and duration of activity peaks displayed seasonal variations as would be expected for red deer. While red deer was in the winter enclosures, activity levels were low. Low winter activity has also been shown in free-ranging red deer (Georgii and Schröder 1983), but the extend might differ. Comparison between all-year free ranging red deer at National Park Bavarian Forest would therefore be useful to assess the full impact of refinement on the activity patterns. Red deer in our study was generally more nocturnal than we expected. The reason for this is not clear yet. It would be useful to compare data from other areas with varying hunting impact to decide whether hunting is the reason for nocturnality or other factors not known at present.

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Figures

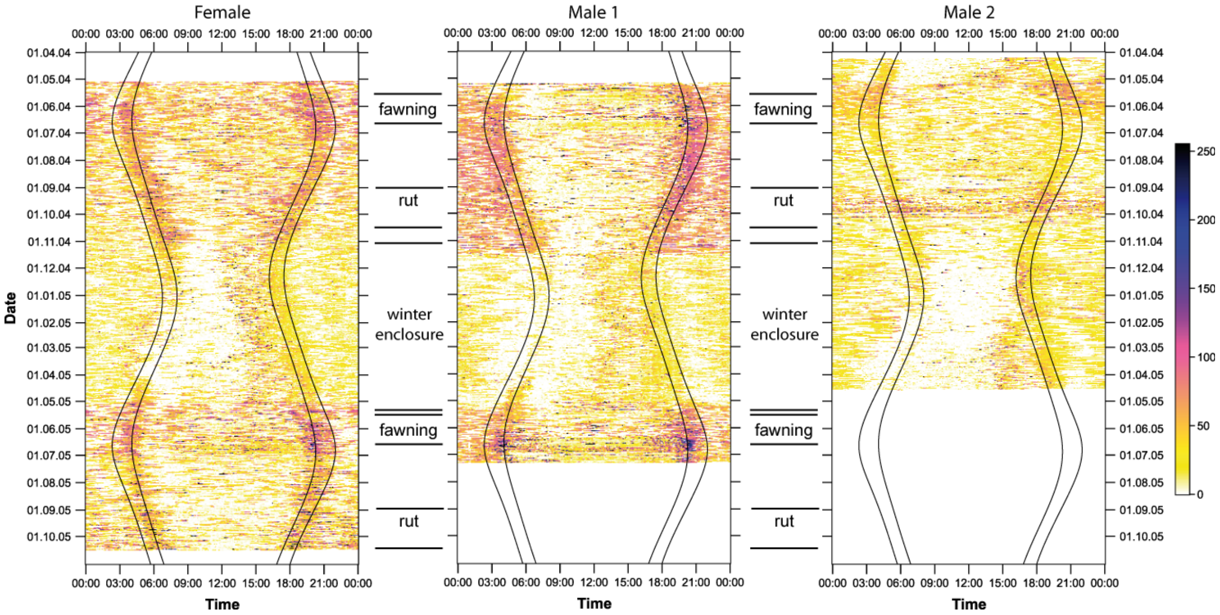

Fig. 1: Exemplary activity plots of one female and two male red deer. Activity has been measured as forward-backwards acceleration on a relative scale from 0 to 255. The level of activity is coded in greyscale intensity. Each horizontal line of the plot represents a single day, days follow each other chronologically from top to bottom. Times are given in CET (Central European Time, UTC +1). Curved lines indicate from left: begin of nautical twilight, sunrise, sunset, end nautical twilight.

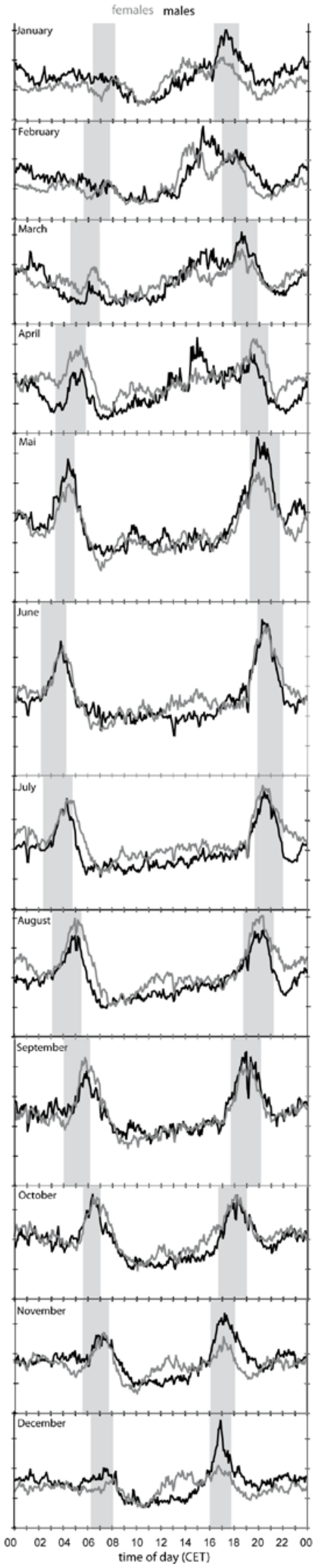

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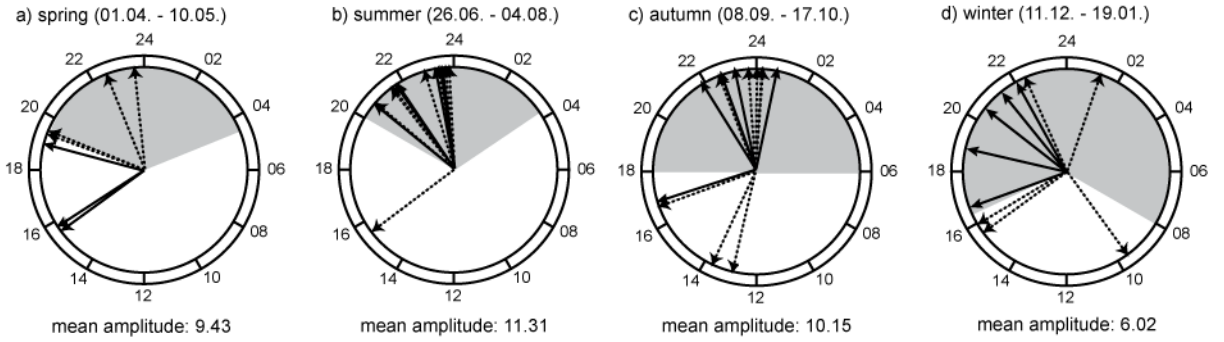
Fig. 2: Monthly form estimates for mean z-transformed activity calculated for females (darkgrey) and males (black). For each five-minute interval, the mean activity was calculated from all days and all animals measured within this month. Grey bars indicate twilight.



a) spring (01.04. - 10.05.)

mean amplitude: 9.43

b) summer (26.06. - 04.08.)

mean amplitude: 11.31

c) autumn (08.09. - 17.10.)

mean amplitude: 10.15

d) winter (11.12. - 19.01.)

mean amplitude: 6.02

Fig. 3: Results of the cosinor analysis of non-z-standardized data for the 24-h-period. The vector points to the time of the acrophase on a 24-hour clock for all individuals (males: black arrows, females: dotted arrows) observed during a period of 30 days. The length of the vector indicates its amplitude (as activity level measured by the acceleration sensor). Since activity values in our study showed distinct individual variation, cosinor amplitude was not numerically analysed. 95% confidence intervals (p = 0.05) are indicated as circles at the tips of all vectors. For all but one individual in summer the 24-hour period was significant.

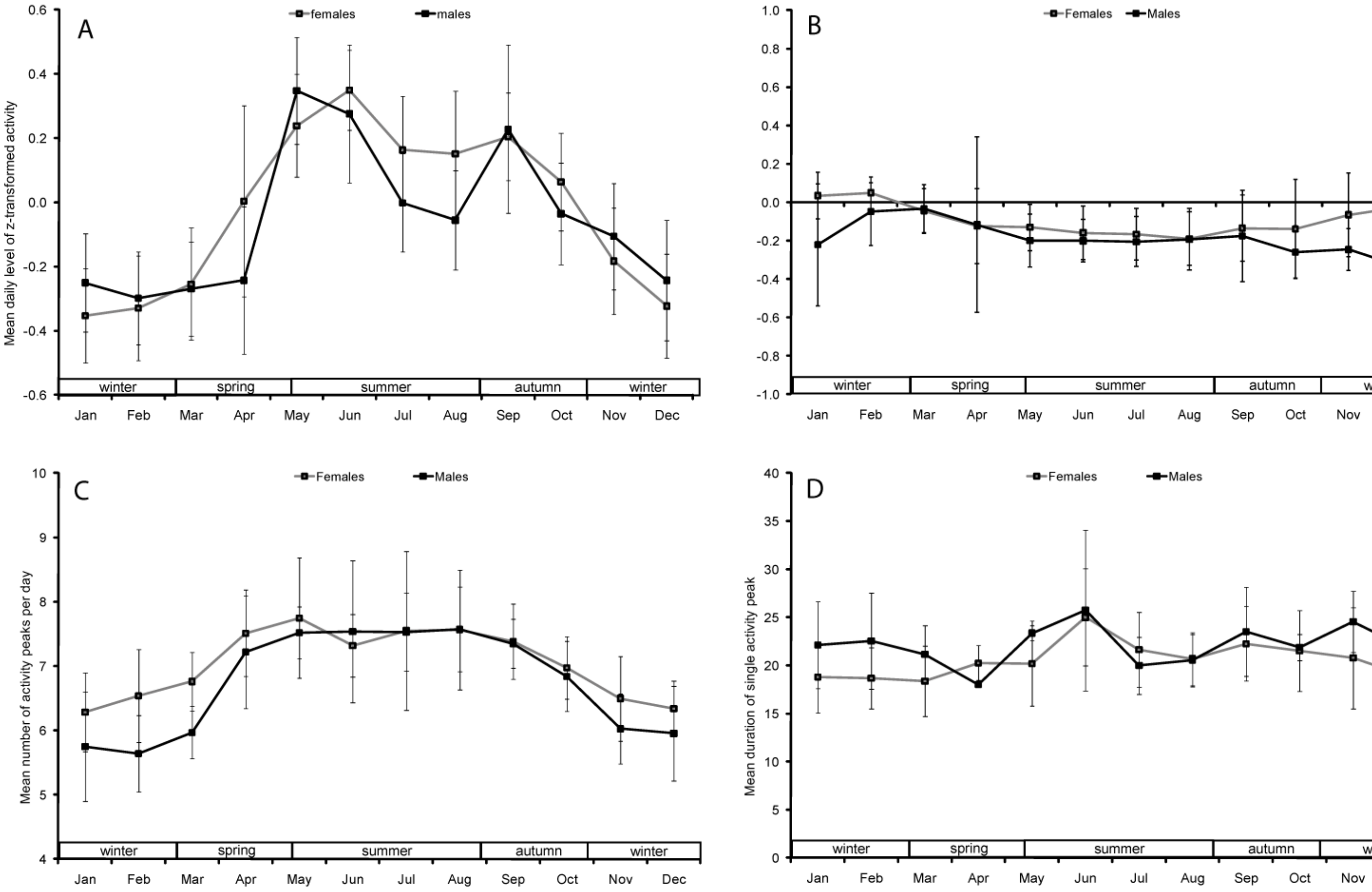


Fig. 4: A, Mean daily sum of z-transformed activity (relative acceleration value) per month as the mean of males (black) and females (dashed). B, Day-night relation of z-transformed activity per month as mean of males (black) and females (dashed). 1 indicates activity level as exclusively diurnal, -1 as exclusively nocturnal, zero as no difference in activity between day and night. C, Mean number of activity peaks per day as mean of males (black) and females (dashed). D, Mean duration of activity peaks per day as mean of males (black) and females (dashed). Error bars in all graphs show standard deviations.

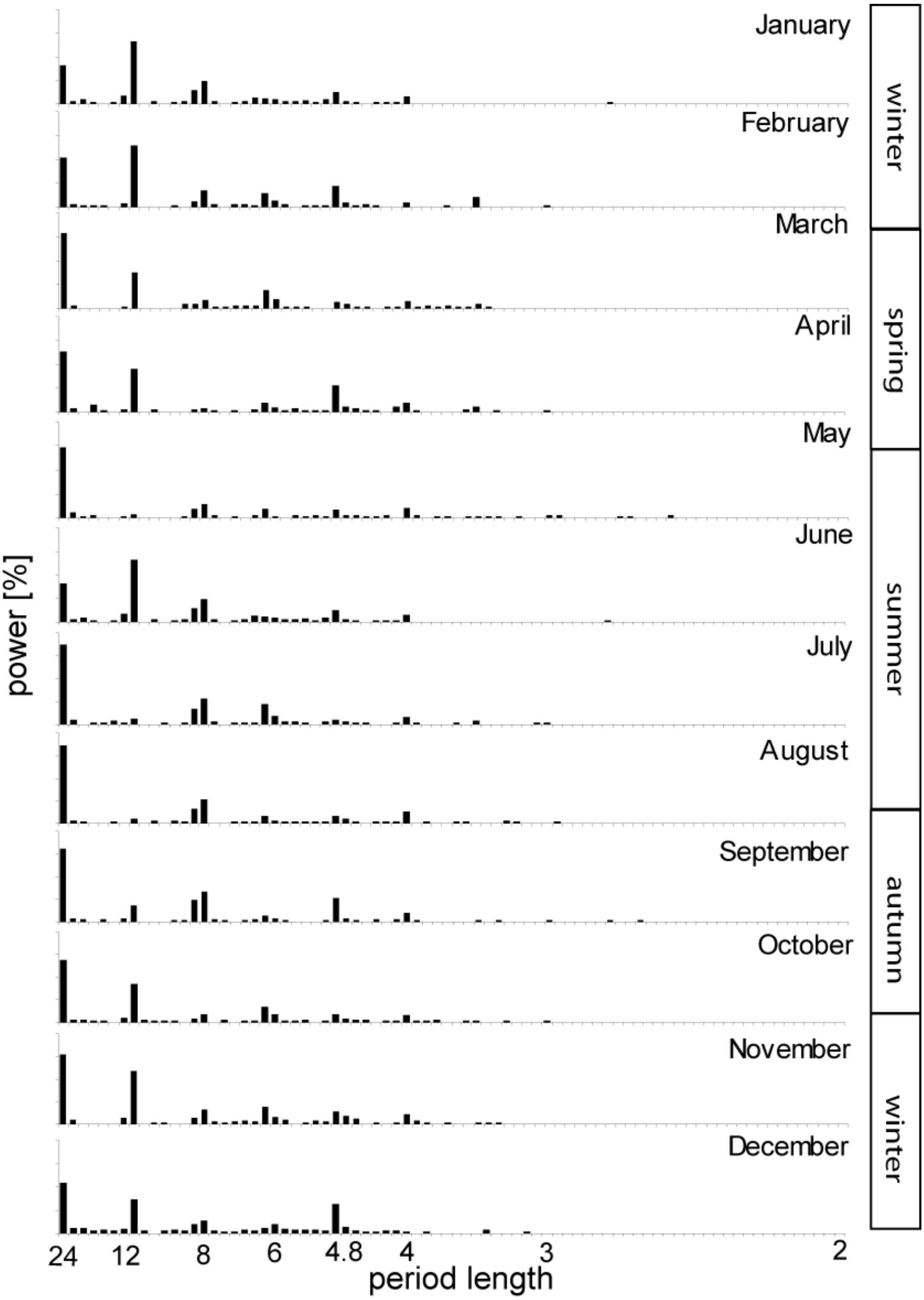


Fig 5.: Plot of the monthly power spectra of red deer activity in Bavarian Forest National Park. Each power spectrum was calculated from 28 day segments. Seasonal variation of the circadian and ultradian (up to period length of 2 hours) spectral components are shown.

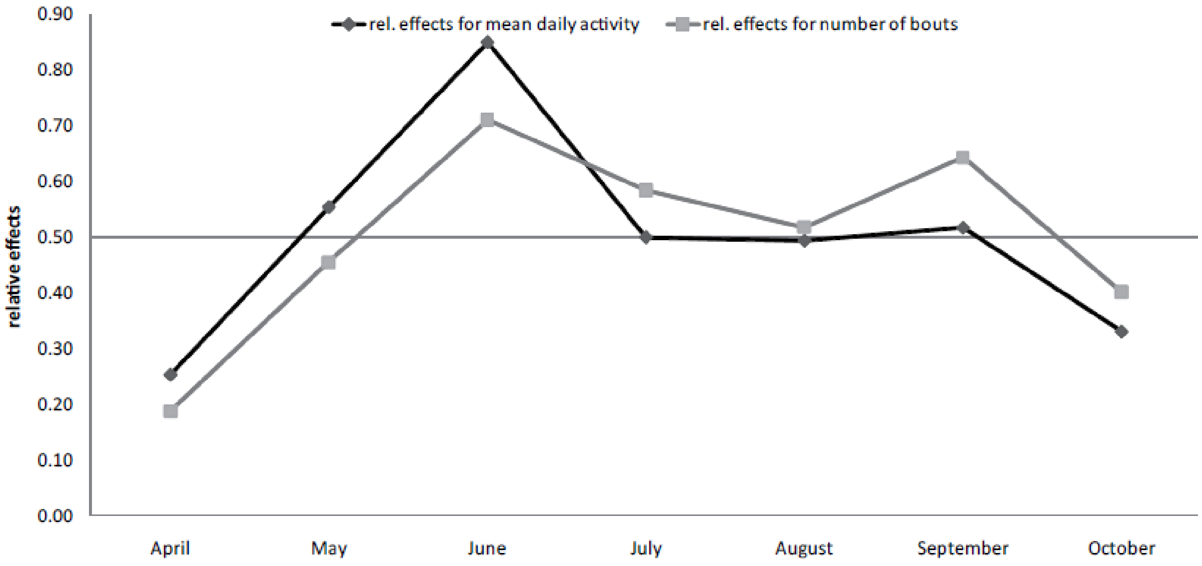


Fig. 6.: The significant relative marginal effects and their 95% confidence intervals (as calculated by the NMM) for the vegetation period. The relative marginal effects provide a graphical representation of effect changes between successive time periods and thus indicate the importance of a particular effect.

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Anlage 7:

Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park

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Abstract

Climate change may directly induce shifts in stand-level dynamics by altering the regeneration, growth and mortality of tree species, and indirectly by modifying interspecific competition. While some experimental and simulation studies have shown that these effects can be compensated by lower browsing pressure, it is not clear how species composition and stand basal area may respond in the short and long term, and to which extent.

We investigated the response of forests to isolated and combined changes of climatic conditions and ungulate browsing intensity in the Bavarian Forest National Park (BFNP), a strictly protected forest reserve. To this aim, we firstly characterized the browsing variability within the BFNP and among each tree species. Based on this, we implemented new equations in the forest gap model ForClim v3.0 and simulated the short- and long-term development of different forest types according to pertinent scenarios of browsing intensity.

The model predicted a large dieback of the dominant *Picea abies* and *Abies alba* due to the increase in summer drought and winter temperatures; these species were progressively replaced by *Fagus sylvatica*. While climate change may have a positive impact on tree diversity in the short term (~100 years), long-term simulations (>1000 years) revealed reduced tree diversity and stand basal area compared to those predicted under current climate. While species composition was strongly dependent on browsing intensity under current climate through the changes in seedling selectivity by ungulates and in light regimes, the trajectory of vegetation development under climate change was not significantly altered by browsing. Even for highly palatable species such as *Abies alba*, an eradication of ungulates could not compensate the decline of drought-intolerant species

We conclude that lower ungulates population may be helpful to promote species diversity in *Picea abies* dominated forest. However this may not be sufficient to compensate for the reduction in basal area and diversity that is induced by climate change.

Keywords

Browsing, climate change, tree diversity, productivity, model

1. Introduction

Many simulation models have been developed to improve our understanding of forest dynamics via the representation of the establishment, growth, and senescence of individual trees in forest gaps (see Bugmann et al. 2001 and Pretzsch et al. 2008 for reviews). Because model applications initially focused on general forest properties that are mostly dictated by the performance of adult trees, they often lack detail for simulating the effects of abiotic and biotic factors on the regeneration of juvenile trees. A special issue concerns ungulate herbivores that can be a key factor influencing the tree species mix and thus long-term forest development by reducing or preventing tree establishment (Côté et al. 2004; Seager et al. 2013). Ungulates can even be the most important driver of meta-community structure in systems without strong abiotic influences (e.g., in warm temperate forests; Suzuki et al. 2013). Indeed, interspecific differences in palatability can lead to large differences in browse damage and potentially to shifts in understory composition towards dominance by less palatable species and eventually also in overstory composition (Côté et al. 2004). For example, several studies have shown that the population dynamics of silver fir (*Abies alba* Mill.), a keystone tree species in many European mountains (Simberloff 1998), was strongly affected by changes in ungulate density in contrast to its main co-occurring species, European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea Abies* (L.) Karst.; Heuze et al. 2005; Klopcic et al. 2010).

Depending on how these variables and parameters are considered in forest succession models, ungulate impacts on simulated stand properties (e.g., species composition, basal area, stem numbers) can be negligible (Kramer et al. 2006; Seagle and Liang 2001) or substantial (Didion et al. 2011; Henne et al. 2013). This discrepancy is mainly due to differences in the identity and density of the ungulate populations, in the characterization of site-, stand- and species-specific selectivity by ungulates and in the formulation of the species-specific relationships between browsing and tree establishment (Seidl et al. 2011). Thus, analyses of the factors that influence habitat selectivity by ungulates (i.e. their probability of presence) and an appropriate quantification of species-specific browsing probability are required for accurately simulating the variability in time and space of browsing probability.

This is of particular importance in the context of a changing environment. As underscored by experimental studies, the effects of biotic agents strongly interact with those of climate change (Post & Pedersen, 2008; Speed et al., 2011). For instance, the positive responses to temperature in high-latitude and high-altitude ecosystems may be eliminated under high browse pressure (e.g., Fisichelli et al. 2012). It can also exacerbate drought-induced deterioration of stands by reducing tree regeneration (e.g., Worrall et al. 2008), which was confirmed by simulation studies (e.g., Didion et al. 2011). Thus, the evaluation of the joint effects of climate change and browsing on forest development needs to consider species-specific direct (e.g., selective browsing, climatic range) and indirect (e.g., light regime, competition) effects.

To address these issues, we used the forest gap model ForClim v.3.0 (Bugmann 1996; Rasche et al. 2012) to simulate forest development in the Bavarian Forest National Park (BFNP) under climate change and different ungulate scenarios. The BFNP is one of the major forest reserves in Central Europe that has not been subject to any forest management over several decades (Heurich et al. 2011). There is great concern about the impacts of high ungulate densities on future forest regeneration and dynamics in combination with likely strong climate change (Heurich 2009). In addition, the availability of high-quality data on both forest properties and ungulate behavior renders the BNFP an ideal test bed for addressing the interactions between ungulates and climate change with respect to short- and long-term forest dynamics. From an applied point of view, projections of future forest properties under scenarios of different browsing intensity would be useful in the BFNP to determine which wildlife management (absolute ungulate density, and constant vs. fluctuating densities) is required to maintain or promote forest biodiversity, or to maintain a particular forest composition despite climate change.

Therefore, the main objectives of this study were (1) to derive equations to assess the site- and species-specific variability in ungulate browsing based on field data from the BFNP, (2) to improve the representation of tree establishment in ForClim, and (3) to assess the impacts of browsing, climate change and their interaction on short- and long-term forest dynamics in the BFNP.

2. Material & Methods

2.1. ForClim description

The gap model ForClim simulates the establishment, growth, and mortality of trees on multiple small forest patches to derive stand-scale dynamics (Bugmann 1996). ForClim has been used for several purposes, from the prediction of short-term stand dynamics to the identification of the current and future potential natural vegetation at the stand scale and across environmental gradients (Bugmann and Solomon 2000; Didion et al. 2011; Rasche et al. 2012).

Tree diameter and height growth are specified as a species-specific maximum that is reduced according to key limiting factors (temperature, drought, light availability, and nitrogen availability; see Rasche et al. 2012). As input the model requires monthly means and standard deviations of temperature and precipitation as well as their cross-correlation (Bugmann 1994). The model predicts species-specific basal area, stem numbers and diameter distributions for thirty European temperate tree species. ForClim v3.0 is based on the assumption that trees establish as saplings with a DBH of 1.27 cm, but this occurs only when specific environmental and biotic conditions are fulfilled. These are represented by binary “establishment flags” for winter temperature (*WTEF*), number of growing degree-days (*DDEF*), light availability (*ALEF*), soil moisture (*SMEF)* and browsing probability (*BPEF*), as described in detail by Bugmann (1996) and Didion et al. (2009). These flags take a value of 1 if current conditions meet the species-specific requirements or 0 if they do not.

2.2. Study area

The BFNP is situated in southeastern Germany along the border to the Czech Republic. It was the first National Park in Germany (1970) and now covers an area of 240 km^2. The area is mountainous, with a variation in elevation between 600 and 1453 m above sea level (a.s.l.). The mean annual temperature is between 6.5 °C in the valleys and 2 °C at higher elevations where winters are usually cold and summers hot (Fig. A. 1). Mean annual precipitation ranges between 830 and 2230 mm without a strong dry period but a considerable amount of precipitation that occurs as snowfall. Snow cover persists for 7 to 8 months at higher elevations and 5 to 6 months in the valleys. Cold air pockets are often present in the valley bottoms, leading to an inversion of the thermal gradient especially in winter (Fig. A. 2).

The main soil types are brown cambisols with a more or less prominent tendency to podzolisation. These acidic soils were formed from weathered material originating in the underlying granite and gneiss layers (Heurich and Neufanger 2005).

The forest is dominated by *P. abies,* which co-occurs with *F. sylvatica* on the slopes, and *A. alba* at low and intermediate elevations. Since the mid-1990s, the forests of BFNP have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*) especially at high elevations (Lausch et al. 2013). By 2010, this had resulted in the death of mature *P. abies* stands over an area of 5800 ha. In stands recently disturbed by bark beetle and wind-throw events (Fischer and Fischer 2009), pioneer deciduous species are also present: mountain ash (*Sorbus aucuparia* L.), sycamore maple (*Acer pseudoplatanus* L.), birch (*Betula sp.*), aspen (*Salix sp.*) and poplar (*Populus sp.*). However, they only represent 3.3% of the total basal area of BFNP (Heurich and Neufanger 2005).

The BFNP is of exceptional importance for the protection of large wildlife species, from lynx (*Lynx lynx*) to capercaillie (*Tetrao urogallus)* and including large ungulates such as red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). In order to preserve the natural diversity of flora and fauna from human activity, and to protect privately owned forests that border the BFNP from wildlife damages, several measures of wildlife management were instituted in the management zone of the park, such as a wildlife population control, a reduction of disturbances by restricting public access to certain areas, or a reduction of winter feeding (more details in Heurich et al. 2011).

2.3. Forest inventory data and stand clustering

5805 forested plots were inventoried across the entire BFNP in 2002. The size of the area in which trees were measured ranged between 25 m^2 and 500 m^2 according to tree diameter breast height (DBH; see Heurich and Neufanger 2005). Species, DBH, height, status (dead/alive), and damages (browsing, snow breakage…) were recorded for each tree. As simulating forest dynamics on each of these plots would be neither feasible nor meaningful, the plot data were grouped into distinct categories (strata) in a two-step procedure. First, they were classified according to four zones that differ in elevation and topographic situation: (1) the valley bottoms (low elevation); plots located at the bottom (2a) or the top (2b) of the slopes, and (3) at high elevation (Table 1). Second, for each of these strata we performed a cluster analysis that minimizes the difference within each stratum (clusters) while maximizing their similarity (for methods see Appendix B).

Nineteen strata were obtained from the cluster analysis (nomenclature detailed in Table 1**)**. They differentiated well the plots according to species composition and structure (diameter distribution; Figs. B. 1 to B. 4), as follows:

- Pure *P. abies* stands affected by bark beetles, with regeneration dominated by *P. abies* (*Ns3*), mixed regeneration (*Nm1*, *Nm2a*, *Nm2b*) or without regeneration (*Nn3*).
- *P. abies* stands with regeneration dominated by *P. abies* (*Ss1, Ss2a, Ss3*), *F. sylvatica* (*Sb2a*), mixed regeneration (*Sm1, Sm2b*), or without regeneration (*Sn1, Sn2a, Sn2b, Sn3*).
- Mixed stands with regeneration dominated by *F. sylvatica* (*Mb2b*), or mixed regeneration (*Mm2a*).
- *F. sylvatica* stands with mixed regeneration (*Bm2a*) or without regeneration (*Bn2b*).

2.4. Spatio-temporal variability of browsing

We used additional forest inventory data collected in different parts of BFNP at different times (1981, 1986, 1991, 1996 and 1998) to assess the spatio-temporal variability of browsing. On each plot, seedlings (height between 0.2 and 1.3 m) were measured in a 25 m^2 circle, and browsing events on the main and lateral shoots were reported for each seedling. A total of 7022 plots that contain seedlings were used for the analysis (by pooling all survey years). The spatio-temporal variability in browsing intensity was assessed using in a two-step procedure described below, assuming that selectivity by ungulates of the stand and of the tree species is constant over time (Boulanger et al. 2009) and across the BFNP.

Firstly, a logistic linear-mixed effect (*lme*) model was used to determine the variables that impact ungulate presence (minimum occurrence of one browsing event; P_{ung}) at the stand scale using the *lme4* package (Bates and Maechler 2009) of the open-source software R (R Core Team 2013). We only chose explanatory fixed variables that can be initialized in the succession model ForClim (see further below) such that the resulting relationships were useful for driving model simulations. For instance, the cover by understory herbaceous plants was not taken into account; while it can be a relevant explanatory variable (Reimoser et al. 2009). The date of the survey was added as a random variable that impacts the intercept of the *lme* model (α). The wildlife management units (‘wildlife control’ versus ‘restricted’ areas) and the distance to winter enclosures were also considered as random effects on the intercept, but not analyzed further. Due to the large sample size, the Akaike Information Criterion (AIC) was chosen as model selection criterion instead of AICc (small sample size correction; Akaike 1983 but see Grueber et al. 2011). To analyze the respective effects of each species on ungulate presence, we used a model averaging approach instead of studying the single best model alone by selecting the models whose cumulative Akaike weights contribute to 95% of the total Akaike weight calculated with all possible models (Grueber et al. 2011) using the *MuMin* package (Barton 2009).

Secondly, we found that species-specific browsing probability ($kBrP_s$, i.e. when ungulates are present;) could not be predicted using logistic models; therefore its variability among species was quantified using beta distributions fitted to the frequency of browsing probability at the stand level (Fig. C. 1**)**. The beta distributions were fitted for the 25 m^2 plots of the empirical data; they notably differ from the 500 m^2 patch size used in ForClim simulations. Consequently, the $kBrP_s$ values needed to be aggregated to correctly assess browsing probability variability at larger spatial scale. The effect on forest dynamics simulated by ForClim when using different spatial aggregation scales for $kBrP_s$ was thus tested systematically (Appendix C**).**

2.5. Changes in the tree establishment sub-model of ForClim

As the number of seedlings at the stand level is strongly related to ungulate presence (Table 2), a seedling bank was implemented in ForClim. The environmental filters are used to update on a yearly basis (*t*) a seedling bank for each of the eight main species (*s*), which also depends on the seedling pool of the previous year (*t-1*), assuming a seedling mortality rate of 10% per year. In order to not strongly increase the complexity and number of parameter of the model, seedling growth and mortality were not simulated explicitly (in contrast to Wehrli et al. 2007):

$$seedlings_{s,t} = 0.9 * seedlings_{s,t-1} + 50 * (WTEF_t * ALEF_t * DDEF_t * IMEF_t * SMEF_t)$$

According to this approach, a maximum of 500 seedlings per species per hectare is obtained, which is close to reality (Appendix D) and at the same time allow us to use the equation that derives from the browsing data analysis to predict $P_{ung,temp}$ (range 0 to 1) at each stand (cf. the equation of the best logistic model in Table 2).

A binary response of P_{ung} (0 or 1) was then defined according to a threshold *thr* that maximized the correct classification rate (mean of the true positive and true negative rates), and minimized the prediction bias (Appendix E). To avoid constant P_{ung} across time while $P_{ung,temp}$ is close to *thr* (e.g., if $P_{ung,temp}$ = *thr* + 0.01 and $P_{ung,temp}$ = constant during several decades, no establishment would occur during the entire period), variability was added to *thr* by generating a random number with a normal distribution

$$P_{ung} = \begin{cases} 1, & P_{ung,temp} \geq \mathcal{N}(thr, sd) \\ 0, & else \end{cases}$$

where *thr* = 0.2919 and *sd* = 0.03 (Appendix E). The resulting annual probability of tree establishment was calculated for each species ($gPest_s$) as follows:

$$gPest_s = kEstP * BPEF_s * (seedlings_s/500)$$

where *kEstP* = 0.1 and $BPEF_s$ is a binary variable defined as:

$$BPEF_s = \begin{cases} 0, & \cup(0,1) < kMorBrP_s \\ 1, & else, and\ if\ Pung = 0 \end{cases}$$

and the mortality probability due to browsing $kMorBrP_s$ depends on the species-specific browsing probability $kBrP_s$ and sensitivity to browsing a_{kbrows}, following the relationship designed in Didion et al. (2011):

$$kMorBrP_s = \left(\frac{kBrP_s}{100}\right)^{a_{kbrow_s}}$$

where $kBrP_s$ is assessed by generating random numbers with a beta distribution function whose parameters $\alpha_{\mathcal{B}s}$ and $\beta_{\mathcal{B}s}$ depend on the species' browsing palatability (Fig. 2), and *x* equals 1, 2 or 20, respectively, depending on the aggregation scale (25, 50 or 500 m^2; see Fig. C. 2):

$$kBrP_s = \left(\sum_{n=1}^{x} \mathcal{B}(\alpha_{\mathcal{B}s}, \beta_{\mathcal{B}s}) \right) / x$$

Finally, the number of trees that establish is randomly chosen using a uniform distribution between 1 and *kEstMax* with

$$kEstMax = (int)\ (0.5 + kEstDens * patchsize + kLa_s)$$

with *kEstDens* being a constant (0.006 $m^{-2}yr^{-1}$), and kLa_s a species-specific index of shade-tolerance (Table 2).

2.5. Stand initialization, climatic and soil data

The composition of the seedling bank and stand structure and composition were initialized using the plot data from the last forest inventory (2002). When necessary, tree number per cohort was converted to integers using a random process. To avoid stochastic 'noise' in the results while maintaining a reasonable simulation time, simulations were performed for 400 plots (each of 500 m^2 size) within each stratum (see Appendix F). Within each stratum, plots were replicated if fewer than 400 plots were available from the empirical data; the 'surplus' patches were randomly sampled without replacement from all plots of the stratum.

In order to obtain reliable long-term climatic data for the study area (see Giesecke et al. 2010), we extrapolated the short-term data from three local weather stations (Arber, Waldhäuser, Kligenbrunn) based on long-term data from Zwieselberg using monthly linear regressions (Fig. A. 1). To consider the effect of elevation on climate and the seasonal changes in the thermal gradient, monthly linear regressions were also used to build monthly climatic data for each stratum based on their respective elevation (Table 1 and Fig. A. 2). To represent the differences in aspect and slope among the strata, we used the model parameter *kSlAsp* [-2 to +2] that affects potential evapotranspiration (PET; Bugmann 1994). On steep north-facing slopes, PET decreases by a maximum of 12.5% (*kSlAsp* = −2) while PET increases by a maximum of 25% on steep south-facing slopes (*kSlAsp*=+2). *kSlAsp* was linearly interpolated for each stratum based on the averaged aspect and slope (Schumacher 2004).

To simulate future climate, we used the regional projected climate change (CC) under the A1B scenario of the IPCC's (2007) Fourth Assessment Report (AR4) generated by the statistical regional climate model WettReg (Enke et al. 2005) that results from downscaling of large-scale climate scenario produced by the General Circulation Model ECHAM5 (Roeckner et al. 2003). The Zwieselberg weather station was used as reference to calculate seasonal climate anomalies for future climate (2075-2100) compared with the baseline (1961-2011; details in Table A. 1). The anomalies of the means, standard deviations, and cross-correlations were added (in case of absolute differences) and multiplied (in case of relative differences) to the current climate, and the weather generator of ForClim (Bugmann 1996) was used to generate a future climate with inter-annual variability for each stratum. For long-term simulations beyond 2100, we assumed that climate remains constant after this date, as post-2100 climate is typically not projected by GCMs.

We used the official soil map of Bavaria (Bavarian Environment Agency, '*Übersichtsbodenkarte*' *ÜBK25*, http://www.lfu.bayern.de) with a map scale of 1:25000, to derive information on soil properties. Soil water content (SWC) was determined for each plot when data were available and averaged for each stratum (Table 1).

2.6. Simulation experiments

As the relationships between browsing and tree establishment were calibrated for the eight main tree species or taxa present in the BFNP (*P. abies*, *F. sylvatica*, *A. alba*, *Sorbus aucuparia*, *Acer sp.*, *Betula sp.*, *Salix sp.*, *Populus sp.*), forest succession was simulated for each stratum considering only these species / species groups.

We firstly tested model accuracy for the BFNP by simulating potential natural vegetation (PNV) under current climatic conditions and medium browsing intensity over the period 1981-2002 (intercept of the logistic model = -1.32; Table 2 and Fig. 1). Starting from bare ground, forest succession was simulated for 2000 years to ensure that the simulated forests were in equilibrium with climatic conditions. The high heterogeneity in forest properties within each elevational band is not due to large different environmental conditions (Table 1) but mainly due to past management and disturbances (windthrows and bark beetle outbreaks); therefore we compared PNV simulated by ForClim for the four elevations under current environmental conditions to current forest properties and to the PNV expected in mountain areas of central and Western Europe.

For each stratum, forest succession over the next 2000 years was simulated starting from the current state of the forest as defined by the inventory data, using a range of scenarios of browsing and CC. Temporal variation of ungulate population density was imitated by varying the intercept of the equation that predicts ungulates presence at the stand scale. Seven browsing scenarios were analyzed considering a constant ungulates density using (1) medium, (2) minimum and (3) maximum density over the period 1981-2002; (4) a total absence of ungulates; and fluctuating density with different wavelengths: (5) 20 years, (6) 50 years, and (7) 100 years (Fig. 1). In order to separate the effects of browsing and CC, one set of simulations was performed by varying browsing pressure but using current climate conditions only. A second set of simulations was performed by varying browsing pressure in combination with CC.

2.7. Ecosystem service metrics

We evaluated the impact of CC and browsing on forest properties at long (2000 years) and short term (during the 400 next years). We focused on changes in aboveground stand basal area (BA) and species composition. Changes in tree species richness and evenness were also assessed by calculating Shannon's diversity index based on the proportion of trees of each species by basal area (p_i):

$$H_{species} = -\sum_{i=1}^{S} p_i\left(ln(p_i)\right)$$

3. Results

3.1. Assessment of the spatio-temporal variability of browsing

The probability of ungulate presence at the stand level, i.e. stand selection at the landscape scale, depended strongly on seedling numbers (Table 2). However, as indicated by the coefficients of the *lme* model, each species featured a different attraction ability. High probabilities of ungulate presence were associated with a large presence of palatable species within the stand (high *kBPU* in Table 2). The impact of *S. aucuparia* presence on stand attraction seemed to be stronger than the one of *Acer*, although their palatability is typically considered to be equivalent. The amount of seedlings of non-palatable species such as *P. abies* did not influence ungulate presence. Unexpectedly, there was no effect of LAI but a positive effect of stand BA that may partially be due to the positive relationship between stand BA and the number of seedlings of *S. aucuparia* and *A. alba* (data not shown). Finally, the probability of ungulate presence decreased with elevation (cf. Fig. D. 3). The best *lme* model did not predict ungulate presence well (51% correct predictions), but it accurately predicted their absence (81% correct predictions; Appendix E). Indeed, the patch size of the browsing surveys (25 m^2) was probably inadequate for accurately assessing stand attraction for ungulates and thus for predicting their presence.

Temporal trends in ungulate presence were revealed by assessing the variability of the intercept that is due to the date of the survey (Fig. 1). Ungulate presence seemed to be highest in 1991, corresponding to a period with a high number of red deer culled in BFNP (Heurich et al. 2012). The decrease since the beginning of the 1990s can be explained by the combined increase of the lynx population in the BFNP and the occurrence of severe winters (Heurich et al. 2012). The decrease in browsing percentage could further be linked to the increase in forest regeneration due to bark beetle outbreaks (Heurich et al. 2011). The low ungulate presence in 1996 can be related particularly to the low temperatures of this year (Fig. A. 1). This negative effect was especially strong because this survey was conducted at high elevations only.

Parameters of the beta distributions used to predict browsing probability for each species ($\alpha_{\mathcal{B}s}$ and $\beta_{\mathcal{B}s}$) were related to species *BPU* (Fig. 2 and Appendix C). $\alpha_{\mathcal{B}s}$ was lower than $\beta_{\mathcal{B}s}$ for species that were not preferred by ungulates (low *BPU*), such as *P. abies*, indicating that $kBrP_s$ was close to zero for most stands. With an increase in BPU, the ratio between $\alpha_{\mathcal{B}s}$ and $\beta_{\mathcal{B}s}$ rose, thus revealing that the number of stands with zero $kBrP_s$ decreased while stands with $kBrP_s > 0.5$ became more frequent.

3.2. Prediction of PNV under current climate for testing model accuracy

In the control run with medium browsing intensity and current climate, the model predicted for the entire BFNP a forest dominated by *P. abies* (65.8%) followed by *F. sylvatica* (16.2%) and *A. alba* (15.8%). Compared with the current state of the BFNP (in 2002), the proportion of *P. abies* was matched well (63.8%), while the simulated abundance of *F. sylvatica* and *A. alba* differed strongly from reality (29.3% of *F. sylvatica* and 3.6% of *A. alba*). Similarly, stand BA simulated by the model was close to measured data (33.9 $m^2 \cdot ha^{-1}$ vs. 33.2 $m^2 \cdot ha^{-1}$). However, when we also included the *P. abies* trees that had been killed by bark beetles during the two last decades, the observed proportion of *P. abies* reached 73.6% and stand BA exceeded 43.4 $m^2 \cdot ha^{-1}$, thus revealing a large underestimation of *P. abies* BA by the model.

The underestimation of stand BA by the model was particularly high at the bottom of the slopes (2a; -15.7 $m^2 \cdot ha^{-1}$ when including dead *P. abies*), which was caused mainly by the underestimation of this species (Fig. 3). At high elevations, *P. abies* BA predicted by the model was also below the one measured before the bark beetle event (23.6 $m^2 \cdot ha^{-1}$ and 41.0 $m^2 \cdot ha^{-1}$, respectively). Simulated variability in BA of *F. sylvatica* and *A. alba* among elevations was quite low. Maximum values of BA simulated for *F. sylvatica* and *A. alba* were reached at the bottom of the slopes for both species (6.5 $m^2 \cdot ha^{-1}$ and 6.8 $m^2 \cdot ha^{-1}$, respectively) and minimum values at high elevations (3.2 $m^2 \cdot ha^{-1}$) and at the top of the slopes (3.5 $m^2 \cdot ha^{-1}$), respectively. In contrast, the forest inventory data reveal a large difference in BA of *F. sylvatica* among elevations (from 12.9 $m^2 \cdot ha^{-1}$ at the top of the slopes to 0.8 $m^2 \cdot ha^{-1}$ at high elevations) and an almost complete absence of *A. alba* at the two higher elevation bands (0.4 and 0.0 $m^2 \cdot ha^{-1}$).

3.3. Future forest dynamics: effects of browsing alone

In the short term, simulations under minimum browsing intensity indicated a slight increase in total stand BA compared to the run under medium browsing intensity (+1.3 $m^2 \cdot ha^{-1}$ for the entire BFNP over 400 years; range between +0.2 $m^2 \cdot ha^{-1}$ and 3.3 $m^2 \cdot ha^{-1}$; Fig. 6). This increase was more pronounced when ungulates were absent (+2.5 $m^2 \cdot ha^{-1}$ on average, range between +0.4 $m^2 \cdot ha^{-1}$ and 3.9 $m^2 \cdot ha^{-1}$). This was mainly due to the rise in *A. alba* BA, and to a lower extent in *F. sylvatica* BA, which were partly compensated by a decrease in *P. abies* BA (Fig. 5; from -0.9 $m^2 \cdot ha^{-1}$ at high elevations to -3.7 $m^2 \cdot ha^{-1}$ at the bottom of the slopes). The simulated increase in tree species diversity was directly related to this reduction in spruce dominance, and thus was higher when browsing intensity was zero (Fig. 6). In contrast, higher browsing intensity did not significantly impact tree species diversity in most strata, and even induced a decrease in tree species diversity in four of them (Fig. 6), i.e. those located at high elevations where higher browsing intensity neutralized the expected increase in *A. alba* BA, and induced an increase in *P. abies* BA while this trend was not evident at the other elevations (Fig. 5).

The PNV simulated under minimum browsing intensity and in the absence of browsing significantly changed from the one simulated under medium browsing intensity, particularly at the bottom of the slopes (Fig. 4). At these elevations, overall BA increased slightly (+2.7 $m^2 \cdot ha^{-1}$ and +5.5 $m^2 \cdot ha^{-1}$ for scenarios 2 and 4, respectively, compared to scenario 1), but species composition changed strongly. The proportion of *A. alba* rose from 21.3% to 33.5% and 44.0% between scenarios 1, 2 and 4, respectively. In contrast, *P. abies* BA decreased from 52.7% to 40.1% and 30.1%, while beech abundance remained nearly constant. Under minimum browsing intensity, *A. alba* reached 23.7% of total BA across the BFNP, and 30.4% in the absence of browsing, while it was respectively lower than 15% and 7% under medium and high browsing intensity.

Temporal variation in browsing intensity had a negligible effect on total BA and species composition, at least for the wavelengths considered here (Appendix G**)**. The number of *A. alba* trees was predicted to be higher than under constant browsing intensity (from +19.5% to +25.8%), but this increase was limited to small DBH classes, leading to increases in BA that were below +1 $m^2 \cdot ha^{-1}$. Similarly, simulation results were not strongly impacted strongly when different aggregation scales were used for in the assessment of species-specific browsing probability at the stand scale (Appendix C).

3.4. Future forest dynamics: effects of climate change alone

Keeping browsing pressure constant at a medium intensity but changing the climate resulted in an abrupt and durable change in species composition (Fig. 5). Compared to current climatic conditions, climate change induced a large dieback of *P. abies* over the next two centuries irrespective of the elevation, but it happened earlier at the bottom of the slopes, i.e. at the driest and hottest sites (Fig. 5). Similarly, *A. alba* was strongly affected by the new climatic conditions as the model did not predict any increase in BA during the next centuries, in contrast to the simulation under current climatic conditions. The model then predicted an increase in BA of *F. sylvatica* during the following two centuries except at the bottom of the slopes, where the BA of this species remained constant. Consequently, tree species diversity increased strongly in most of the stands due to the reduction in *P. abies* dominance and a higher evenness in species composition (Fig. 6).

In the long term, the model predicted a strong reduction in stand BA at PNV when moving from current to new climatic conditions (from 34.1 $m^2 \cdot ha^{-1}$ to 22.9 $m^2 \cdot ha^{-1}$; Fig. 4). Only *F. sylvatica* and, to a lower extent, *Acer sp.* and *Populus sp.* were able to survive under these hotter and drier conditions, leading to a reduction in tree species diversity (Shannon's index for PNV averaged 0.86 and 0.75 under current and new climatic conditions, respectively).

3.5. Future forest dynamics: effects of climate change and browsing

Even though reduced browsing intensity promoted the establishment of *F. sylvatica* and *A. alba* establishment at the coldest and wettest site (high elevation), it did not compensate for the decrease in total stand BA that was induced by climate change (Fig. 5). The increase in BA ranged between +2 $m^2 \cdot ha^{-1}$ and +4 $m^2 \cdot ha^{-1}$ according to browsing scenario, stratum, and elevation; this was minor compared to the overall decrease in BA of 12.4 $m^2 \cdot ha^{-1}$ across the BFNP that was due to climate change (scenario 1; Fig. 6). Overall, only 27% of the decrease in BA would be compensated by completely eradicating browsing. Indeed, the decline in *P. abies* BA that was predicted for the two next centuries occurred at the same speed and extent irrespective of the browsing scenario (Fig. 5). Similarly, the negative effect of higher browsing intensity on stand BA was negligible compared to the effects of climate change. Similarly, changes in tree species diversity due to climate change were little impacted by changes in browsing intensity, although they were related negatively (Fig. 6).

The effects of changing browsing intensity on forest properties for the PNV were more limited under climate change than under current climatic conditions (Fig. 4). The reduction in browsing from high intensity to an absence of ungulates induced an increase in stand BA from 21.9 $m^2 \cdot ha^{-1}$

to 26.2 $m^2 \cdot ha^{-1}$ in the BFNP, which was mainly due to higher establishment rates for *F. sylvatica*, while species composition remained nearly unaffected.

4. Discussion

4.1. Browsing variability in space and according to tree species

The probability of ungulate presence at the stand level, which determines habitat selection at the landscape scale, depended strongly on seedling number. This pattern is commonly observed in large herbivores (van Beest et al. 2010), with a different magnitude according to the tree species. High probabilities of ungulate presence were associated with a large abundance of palatable species within the stand, such as *S. aucuparia*, *Acer sp.* or *A. alba*, while ungulate presence was not related to the abundance of *P. abies*. In the BFNP, stands with high BA were favored by deer as they contain more seedlings of *S. aucuparia* and *A. alba* and because they offer protection from predators during daytime and thermal cover during the nights and in winter (Godvik et al. 2009). The probability of ungulate presence decreased non-linearly with elevation due to thicker snow cover and lower temperatures in spring that reduce ungulate movement and the length of the period when seedlings are available (Cagnacci et al. 2011). This trend may also be related to wildlife management and other human activities, as low-elevation stands are close to agricultural areas or meadows with high quality resources (see Bonnot et al. 2013), and to feeding stations outside of the BFNP. Because of the design and spatial scale of the survey data, several potentially important factors could not be considered, including (i) habitat quality of the surrounding area (Reimoser et al. 2009), (ii) the timing of the survey within the year (Heurich 2009), and (iii) understory herbs, forbs and grasses (Boulanger et al. 2009). Therefore, the linear mixed-effects model did not assess the probability of ungulate presence very accurately. However, it reproduced the temporal and spatial variability of the probability of ungulate presence within and among each stratum in a reasonably consistent manner.

Seedling selectivity by ungulates within a stand also depended on species palatability, as revealed by the different parameters of the beta distributions. When ungulates are present in a stand, they prefer to browse *A. alba* or *S. aucuparia,* but very rarely choose *P. abies*. This pattern was commonly reported in temperate and mountainous forests (e.g. Ammer 1996) and was the main cause of the inter-specific variability in browsing probability in our study, too.

4.2. Prediction of the PNV under current climate for testing model accuracy

Under current climate and medium browsing intensity, the model simulated the expected forest types with acceptable accuracy. Dominance by *P. abies* was reproduced as well as the effect of elevation on the presence of *F. sylvatica*. Even though simulated stand BA was lower than the one measured before the bark beetle outbreaks (especially for spruce) and the proportion of *A. alba* was higher than that currently observed, this does not indicate that the model should not be used in the BFNP, because forest properties before the bark beetle outbreaks were far from being representative of the PNV in this area. *P. abies* was most likely over-represented strongly in the BFNP due to intense forest management between the 16th century and the foundation of the BFNP (cf. Heurich and Englmaier 2010). The past promotion of this drought-sensitive species resulted in a disequilibrium between species composition and climate (Temperli et al. 2012).

The PNV predicted by the model was more typical of old-growth temperate forests from central Europe and mountain areas of Western Europe, which are characterized by a high proportion of *A. alba* and *F. sylvatica* (e.g., Ammer 1996; Vrška et al. 2009). This was confirmed by the pollen analyses in the BFNP, which indicated that forests were originally dominated by *A. alba* and *F. sylvatica* (e.g., strata *Mm2a* or *Mb2b* in Appendix B), while *P. abies* was limited to specific locations such as peat bogs and rocky areas, or higher elevations (Heurich and Englmaier 2010).

The proportion of *F. sylvatica* on the slopes (i.e., at intermediate elevations) should have been higher than predicted. This anomaly was not caused by the implementation of the seedling bank, as this change led to an increase in tree establishment rates due to lower influence of inter-annual variability in climatic conditions (Fig. D. 4). However, it was probably due to underestimated tree establishment rates caused by inaccurate species-specific parameters related to establishment, and especially to limitation by winter temperature. For example, at the warmest site (bottom of the slopes), where the proportion of *F. sylvatica* should be high, minimum winter temperatures fell below the lower limit for beech establishment (-4 °C) for 65% of the years, thus strongly hindering establishment of this characteristic species. This anomaly may be due to the fact the estimation of the winter temperature thresholds did not consider snow cover constraints experienced by the seedlings, or due to an overestimation of *F. sylvatica* frost sensitivity.

4.3. Effects of changes in browsing under current climate

Reduced browsing intensity caused a slight increase in stand BA that was more pronounced in the scenario without any browsing. This also led to a large change of species composition directly through the selection of palatable species by deer, and indirectly via the alteration of the light regime (Vavra et al. 2007).

As expected, *A. alba* was the main beneficiary of a reduction in browsing intensity. Its proportion rose from 7% to 30% of total BA and even reached 44% in some stands. This species combines both high selectivity by deer at large and small spatial scales, and high sensitivity to browsing (Ammer 1996; Klopcic et al. 2010; Didion et al. 2011; Kupferschmid and Bugmann 2013). Thus, it is usually considered as the most heavily browsed of the commercially important tree species in mountain forests of central Europe, and numerous studies have shown that its regeneration can be poor for decades due to browsing (Senn and Suter 2003). However, even under high browsing intensity (maximum intensity of the period 1981-2002), the model did not predict an extinction of this species in the BFNP, while several authors indicated that silver fir extinction could occur in strictly protected forest reserves (e.g., Vrška et al. 2009). In contrast, *P. abies* seedlings are usually avoided by ungulates and are highly resilient to browsing. Thus, its proportion increased with higher deer populations that removed potential competitors. However, as it is an intermediately shade-tolerant species, its establishment and growth rates were negatively impacted by reduced browsing intensity through more intense competition for light.

Although stand BA did not change considerably thanks to the partial offset between *A. alba* and *P. abies* BA, tree species diversity was modified strongly by the change in ungulate pressure. Clearly, herbivory tends to replace palatable species (e.g., *A. alba*) by unpalatable ones (e.g., *P. abies*), resulting in reduced tree species diversity (Horsley et al. 2003; Vavra et al. 2007). This is especially true when unpalatable species already dominate the forest, such as in the BFNP.

4.4. Effect of changes in climate

The increase in summer drought and winter temperatures had a substantial impact on species composition and stand BA.

As climate was changing, the disequilibrium between *P. abies* abundance and climate increased, ultimately resulting in stress-induced mortality, as predicted for other areas of Germany (e.g., Albert and Schmidt 2010; Temperli et al. 2012). Because of its relatively low tolerance of summer drought, *A. alba* faces a high risk of a contraction of its distribution range due to climate change. Most species distribution models parameterized using *A. alba*'s current distribution area agree on this (e.g., Falk and Mellert 2011). Interestingly, the increase in winter temperatures was projected to play an important role in the BA decline of both species. As revealed by experimental studies and other process-based modelling approaches, climate warming may cause abnormal bud burst due to the lack of chilling (Hänninen and Tanino 2012; Morin et al. 2009). In ForClim v3.0, successful *A. alba* regeneration requires a mean temperature of the coldest month below -3 °C (details on the parameterization in Bugmann and Solomon 2000), which was fulfilled in 70% of the years under current climate, but only in 13% of the years when winter temperatures increased by ca. 3.8 °C (high elevation stands; this percentage amounted to 52% for *P. abies*).

In contrast to other simulation studies (e.g., Temperli et al. 2012), the dieback of drought-sensitive species increased forest diversity in our study. This was particularly true for the strata with large current dominance by *P. abies*, revealing that climate change effects on species diversity may strongly depend on current diversity. The reduction in competition intensity due to the dieback of *P. abies* and *A. alba* directly induced higher establishment rates of light-demanding species and indirectly was of benefit to *F. sylvatica* and *Acer sp.* whose establishment and growth also profited from higher temperatures (Albert and Schmidt 2010). However, under medium browsing intensity, species replacement did not offset the dieback of drought-sensitive species. Moreover, as *F. sylvatica* became increasingly dominant in the simulations and outcompeted light-demanding species, Shannon diversity gradually diminished after 2150 until a level similar to the one currently observed was reached.

4.5. Combined effects of browsing and climate change

This study reveals that anthropogenic changes in climatic conditions are likely to be more critical than changes in browsing intensity in spruce-dominated forests such as those in the BFNP. Overall, the trajectory of vegetation development under climate change was not significantly altered by browsing. Only 27% of the decrease in BA due to climate change was compensated when browsing was eradicated completely (which would be highly unlikely to be implemented in reality). Similarly, the shift in composition to a forest dominated by *F. sylvatica* rather than *P. abies* was not impacted by browsing. Furthermore, the positive responses to higher temperature and light availability by *F. sylvatica* recruitment and growth were not eliminated under high browsing pressure because of the intermediate palatability and sensitivity to browsing of this species (in contrast to *Acer sp.*; see Fisichelli et al. 2012). Lastly, a reduction in ungulate population density may not compensate stress-induced *P. abies* and *A. alba* dieback as (i) *P. abies* recruitment does not usually depend on ungulate browsing, and (ii) the new climatic conditions would not match the water and chilling requirements of either species any more.

4.6. Methodological considerations and limitations

The present simulation study identified several aspects that need to be considered in modelling approaches that aim to predict and disentangle the relative effects of climate change and browsing on forest dynamics.

First, the spatial variability in ungulate presence at the stands scale should be assessed, as browsing can differently impact forest development depending on the initial state of the forest (strata) and its elevation. This requires an accurate empirical assessment of stand-specific and species-specific browsing variability, which was available to us for the BFNP. “Data-free” assumptions on browsing intensity, in contrast, may lead to biased results, such as an overestimation of the interactive effects of browsing and climate change (e.g. in the spruce-dominated forest of Didion et al. 2011).

Second, oscillations in browsing intensity did not lead to sustained compositional shifts when the establishment of species sensitive to browsing was limited by other factors already (in contrast to the findings by Didion et al. 2009 or Sage et al. 2003).

These results are all the more important if the study focus is on the short-term development of forest properties. The assessment of the spatio-temporal variability in ungulate density could be improved via a more mechanistic approach (e.g., Seidl et al. 2011), either by simulating more accurately habitat selectivity by ungulates using understory vegetation and stand topography (Reimoser et al. 2009), and by a better prediction of ungulate population dynamics. A mechanistic model of deer density that considers sex ratio, reproductive rates and mortality rates (e.g., Millington et al. 2013) would be valuable for predicting long-term changes in ungulates population sizes and forest dynamics. However, a first step would be to add direct feedbacks between both components (e.g., via foliage biomass and palatability: Kramer et al. 2006). A better quantification of the species-specific and site-specific responses of seedlings to browsing would also be quite useful to improve the predictions of coupled plant-ungulate systems (cf. Kupferschmid and Bugmann 2013).

Clearly, our results should not be mistaken as predictions of the future state of the BFNP, but rather as an evaluation of possible future trends and the importance of the processes shaping long-term forest dynamics. Indeed, the representativeness of the period 1981-2002 for simulating browsing pressure and its temporal variation is probably not covering the full range of natural variability. Moreover, the predicted decline of *A. alba* due to climate change is probably overestimated. As revealed by a recent paleo-ecological synthesis (Tinner et al. 2013), *A. alba* has the potential to co-dominate the Mediterranean vegetation (e.g. with *Quercus ilex* or *Acer sp*.) if fire, windthrow and browsing are not excessive, and it was also found at high elevations beyond its current distributional limit across the Holocene. Thus, its temperature and drought tolerance are probably higher than commonly thought. An improved parameterization of this species is thus needed, for instance using past distribution range or ecophysiological data to better represent its obvious genetic adaptive capacity and its phenotypic plasticity. Finally, as the relationship between stand properties and browsing probability was calibrated based on data for the eight main tree species (or taxa) of the BFNP only, the immigration of other species could not be considered. This omission probably induced an underestimation of stand BA and Shannon diversity in the driest and hottest stands, as these may be colonized by drought-tolerant species such as *Quercus sp.* or *Pinus sylvestris* (Didion et al. 2011).

4.7. Implications for forest management and nature conservation

A. alba is considered an important structural and functional component of European forests and often serves as a keystone species for maintaining high biodiversity (Simberloff 1998). As discussed above, the proportion of this shade-tolerant species is projected to rise in the BFNP due to the reduction in human interventions. However, large *A. alba* (and *P. abies*) diebacks are likely to occur during the coming two centuries in the BFNP if climate changes as fast as is expected (IPCC 2007). As shown by Nourtier et al. (2013) regarding *A. alba*, local topography and the spatial heterogeneity in soil properties can compensate for the negative effects of climate change on tree growth and mortality. Thus, *A. alba* and *P. abies* populations may in the future be limited to micro-refugia that would support locally favorable climates amidst unfavorable regional climates (Dobrowski 2011). As these species are unlikely to disappear from the area, measures of ungulate limitation through regulated hunting or the promoted return of large predators such as lynx may be still of key importance to support *A. alba* in the BFNP. However, our study emphasize that forest management tools of both natural and productive forests from Central Europe should be re-evaluated, and should be more devoted to compensate for negative effects of climate change than browsing ones.

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Figures caption

Fig. 1: *Left:* Conditional means and standard deviation of the effects of the survey date on the intercept of the *lme* model used for predicting P_{ung} (mean intercept = -1.32; cf. **Table 2**). *Right*: Changes in the intercept imposed for each browsing scenario: Constant medium (scenario 1), minimum (scenario 2) and maximum browsing intensity (scenario 3) are shown in green, blue and in red, respectively. Three scenarios of fluctuating browsing intensity with similar mean, maximum and minimum values but different wavelength were also tested (wavelengths of 20, 50 and 100 years for the scenarii 5, 6 and 7). Scenario 4 corresponds to a total absence of ungulates.

Fig. 2: Effect of browsing preference by ungulates for the different tree species (BPU; **Table 2**) on the parameters of the beta distributions ($\alpha_{\mathcal{B}s}$ and $\beta_{\mathcal{B}s}$). They were used to predict species-specific browsing probability for *Picea abies* (dark blue), *Betula* sp. (grey), *Fagus sylvatica* (green), *Populus* sp. (orange), *Sorbus aucuparia* (light blue), *Abies alba* (purple), *Acer* sp. (red), and *Salix* sp (pink; see details in **Appendix C**). The latter four species have the same BPU (small gap for graphical reasons). The 95% confidence intervals were calculated using non-parametric bootstrap re-sampling (5000 re-samples). The dashed lines represent linear regressions between beta parameters and BPU ($\alpha_{\mathcal{B}s} = 0.07 + 0.05 \cdot \text{BPU}$; $R^2<0.01$; $p>0.1$; and $\beta_{\mathcal{B}s} = 0.55 - 0.05 \cdot \text{BPU}$; $R^2=0.05$; $p>0.1$). As the number of plots (*n*) for fitting the beta distributions differed among species, we used linear regressions that consider “species weight”: for each species we randomly chose *n* values for $\alpha_{\mathcal{B}s}$ and $\beta_{\mathcal{B}s}$ into the 5000 bootstrap samples and used these points to calculate the linear regressions that were used in the model (solid lines; $\alpha_{\mathcal{B}s} = -0.00 + 0.07{*}\text{BPU}$; $R^2=0.37$; $p<0.001$ and $\beta_{\mathcal{B}s} = 0.65 - 0.08{*}\text{BPU}$; $R^2=0.68$; $p<0.001$).

Fig. 3: Species composition currently observed (O) and PNV simulated by ForClim under medium browsing intensity (S; after 2000 years of simulation from bare ground) for the four elevational bands of the BFNP from low (1) to high elevations (3). Species grouped into the “others” category failed to contribute more than 2% of total stand basal area.

Fig. 4: Segment diagrams showing BA of *P. abies*, *A. alba*, *F. sylvatica* and other species at the initial state (forest inventory of 2002, leftmost column) and at pseudo-equilibrium under current climate (center four columns) and considering climate change (four columns at the right). In the latter two categories, the black open segments represent the current state of the forest to facilitate the comparison with the current state.

Fig. 5: Leftmost column: Short-term development of total BA (black) and BA of *P. abies* (blue), *A. alba* (purple), *F. sylvatica* (green), and the others species (pink) simulated under medium browsing intensity (scenario 1) at the four elevational bands (rows). The three other columns represent the difference in BA of these components under scenarios 2, 3 and 4 relative to scenario 1. Simulations were conducted under current and new climatic conditions, which are indicated by the solid vs. dashed lines, respectively.

Fig. 6: Leftmost column: Short-term development of stand BA (rows 1 and 2) and Shannon diversity (rows 3 and 4) of non-disturbed (black) and disturbed strata (red) simulated with an medium browsing intensity (scenario 1) under current climate (no climate change; rows 1 and 3) and new climatic conditions (with climate change; rows 2 and 4). The three other columns represent the difference in BA and Shannon diversity of the scenarios 2, 3 and 4 relative to scenario 1.

Table 1: Average and standard deviations of altitude, slope and aspect of each stratum defined at high elevation (3), at the top (2b) and bottom of the slopes (2a), and at low elevation (1). Stratum nomenclature: Upper- and lowercase indicates the species composition of the adult and regeneration stages, respectively. *S* indicates that the adult stage is dominated by spruce and *B* by beech, while *M* refers to a mixed composition and *N* indicates that there are several tree species in this developmental stage. Species composition of each stratum is detailed in **Fig. B1** to **Fig. B4** in **Appendix B**.

Stratum	**Nb plots**	**Altitude (m)** Mean ± sd	**Slope (°)** Mean ± sd	**Aspect (°)** Mean ± sd	**kSlAsp**	**SWC (cm)**	**Current BA** ($m^2 \cdot ha^{-1}$)
Ss3	119	1196 ± 66	8.4 ± 5.0	191 ± 109	0.74	10.2	35.3
Sn3	311	1212 ± 60	10.2 ± 5.3	184 ± 102	0.97	9.9	30.7
Ns3	77	1206 ± 64	9.7 ± 5.8	181 ± 101	0.97	10.2	22.0
Nn3	423	1224 ± 59	10.2 ± 5.8	177 ± 95	1.05	9.8	0.6
Sm2b	422	1036 ± 76	12.5 ± 5.2	189 ± 89	1.02	13.7	33.0
Sn2b	614	1018 ± 78	12.7 ± 5.3	194 ± 90	0.98	13.8	44.7
Mb2b	343	1031 ± 83	13.5 ± 4.9	190 ± 82	1.06	14.2	43.0
Nm2b	533	1049 ± 80	13.2 ± 5.5	191 ± 74	1.03	13.4	19.5
Bn2b	191	1019 ± 77	15.0 ± 5.2	194 ± 77	1.09	14.3	39.1
Ss2a	62	790 ± 71	9.0 ± 4.3	198 ± 86	0.72	11.1	38.2
Sb2a	277	806 ± 62	9.6 ± 3.9	204 ± 78	0.70	11.0	41.4
Sn2a	712	797 ± 66	9.2 ± 4.1	198 ± 86	0.74	10.9	44.4
Bm2a	541	804 ± 58	9.8 ± 4.1	199 ± 79	0.78	11.2	37.7
Mm2a	182	800 ± 64	9.6 ± 4.1	199 ± 81	0.76	11.1	38.8
Nm2a	76	793 ± 78	8.9 ± 3.6	199 ± 81	0.70	11.0	20.9
Sm1	179	750 ± 80	5.7 ± 3.2	173 ± 89	0.61	12.5	40.0
Ss1	178	739 ± 68	3.8 ± 2.7	171 ± 87	0.51	16.1	37.5
Sn1	349	751 ± 66	4.6 ± 3.2	170 ± 86	0.51	14.0	45.2
Nm1	216	769 ± 87	4.7 ± 3.4	186 ± 87	0.44	13.5	20.8

Table 2: Results of the best logistic linear mixed-effects (*lme*) model and of the averaging approach for predicting the probability of ungulate presence. The number of seedlings and the observed browsing probability used to derive these models are also provided. Significant effects of both modeling approaches are indicated in dark grey. Est. = Estimate; [CI 95%] = Confidence Interval at the significance level of 95%. As values of all variables were standardized before the *lme* model averaging procedure, model estimates are not comparable to those of the best *lme*. Topographic zone: from low (1) to high elevation (4). “Others” indicates the other species (e.g., *Lonicera nigra*) and seedlings whose species was not correctly defined (e.g., hardwood species). Some parameters used in ForClim are also given: the browsing preference by ungulates (*kBPU*) ranges between 1 (unpalatable) to 5 (highly palatable and preferred browse; from Didion et al. 2011). *kBrow* assesses seedling sensitivity to browsing and considers the species’ *BPU*, the rate of height growth of seedlings, the ability of a tree species to compensate for tissue losses, and its survival probability (Didion et al. 2011). Species’ shade tolerance (*kLa*) ranges between 1 (shade-tolerant) and 9 (light-demanding).

Logistic LME model **0: Absence** **1: Presence** **N = 7022**		Browsing survey database		Best model	Model average (43 models on 2048)	Species-specific parameters in ForClim		
		Nb seedlings	Obs. BrP	Est.	[CI 95%]	kBPU	kBrow	kLa
AIC				7649				
Intercept				**-1.32**	[-2.99 -0.13]			
Number of seedlings (10^{-4})	Nb S. aucup.	4574	0.33	**4.67**	[1.04 1.37]	5	4	7
	Nb P. abies	14042	0.05		[-0.04 0.18]	1	2	5
	Nb F. sylv.	8000	0.15	**0.09**	[0.10 0.34]	3	3	1
	Nb A. alba	2579	0.24	**2.71**	[0.40 0.66]	5	5	1
	Nb Acer sp.	891	0.43	**3.08**	[0.33 0.75]	5	4	4
	Nb Betula sp.	204	0.15	**2.71**	[0.02 0.25]	2	1	9
	Nb Salix sp.	48	0.19	**7.78**	[0.01 0.34]	5	2	5
	Nb Populus sp.	31	0.13		[-0.17 0.11]	4	2	5
	Others	989	0.28					
Stand BA (10^{-3})				**9.0**	[0.05 0.37]			
LAI					[-0.27 0.24]			
Topographic zone (10^{-3})				**-8.77**	[-0.17 0.09]			

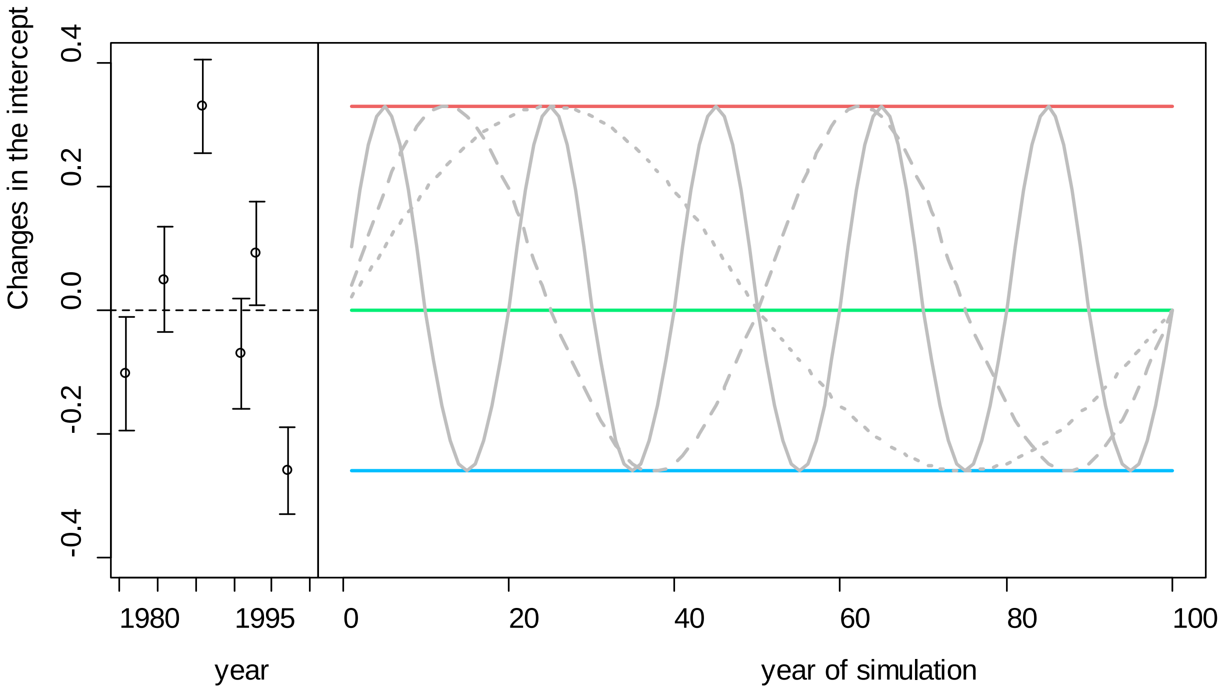

Changes in the intercept
0.4
0.2
0.0
-0.2
-0.4
1980
1995
year
0
20
40
60
80
100
year of simulation

Fig. 1

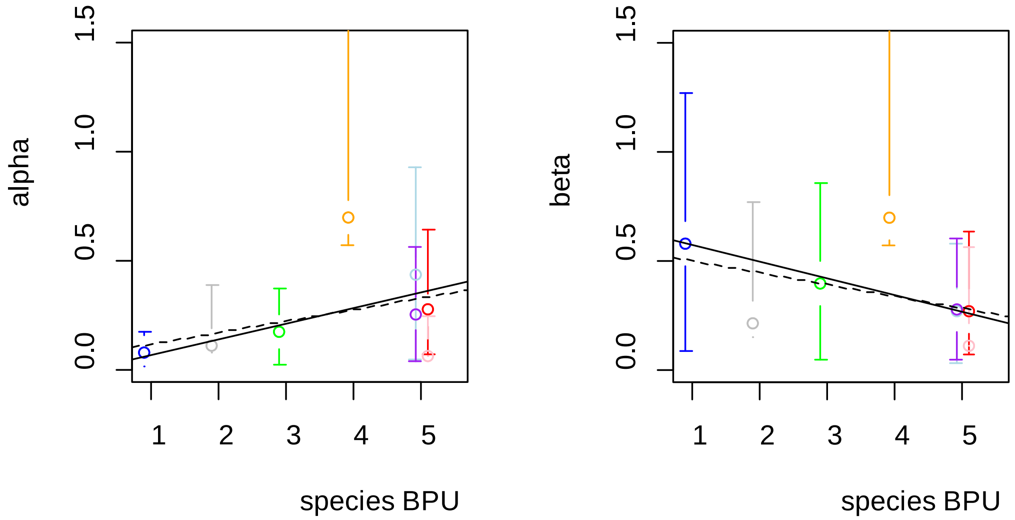

alpha
1.5
1.0
0.5
0.0
1
2
3
4
5
species BPU
beta
1.5
1.0
0.5
0.0
1
2
3
4
5
species BPU

Fig. 2

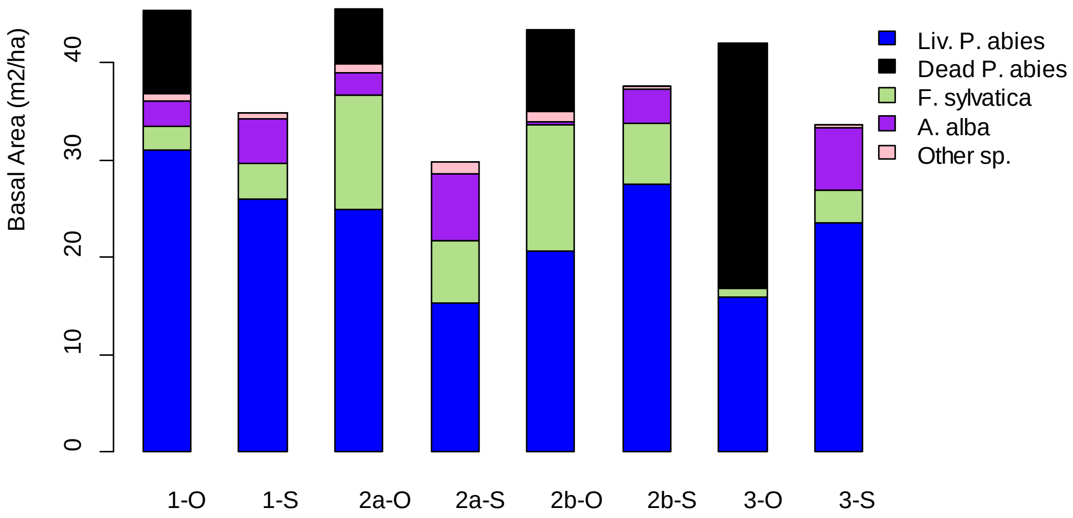

Basal Area (m2/ha)
0
10
20
30
40
1-O
1-S
2a-O
2a-S
2b-O
2b-S
3-O
3-S
Liv. P. abies
Dead P. abies
F. sylvatica
A. alba
Other sp.

Fig. 3

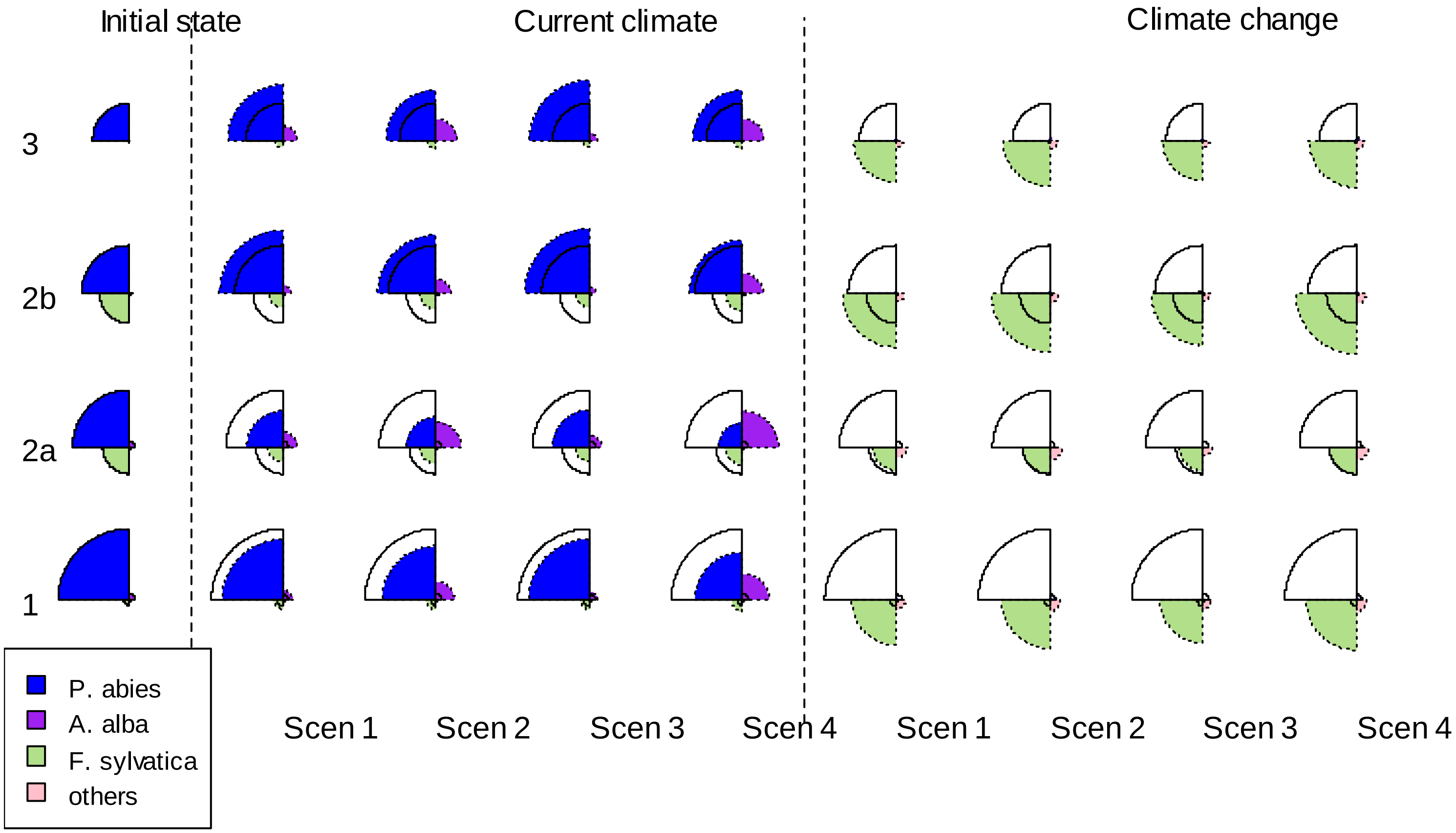
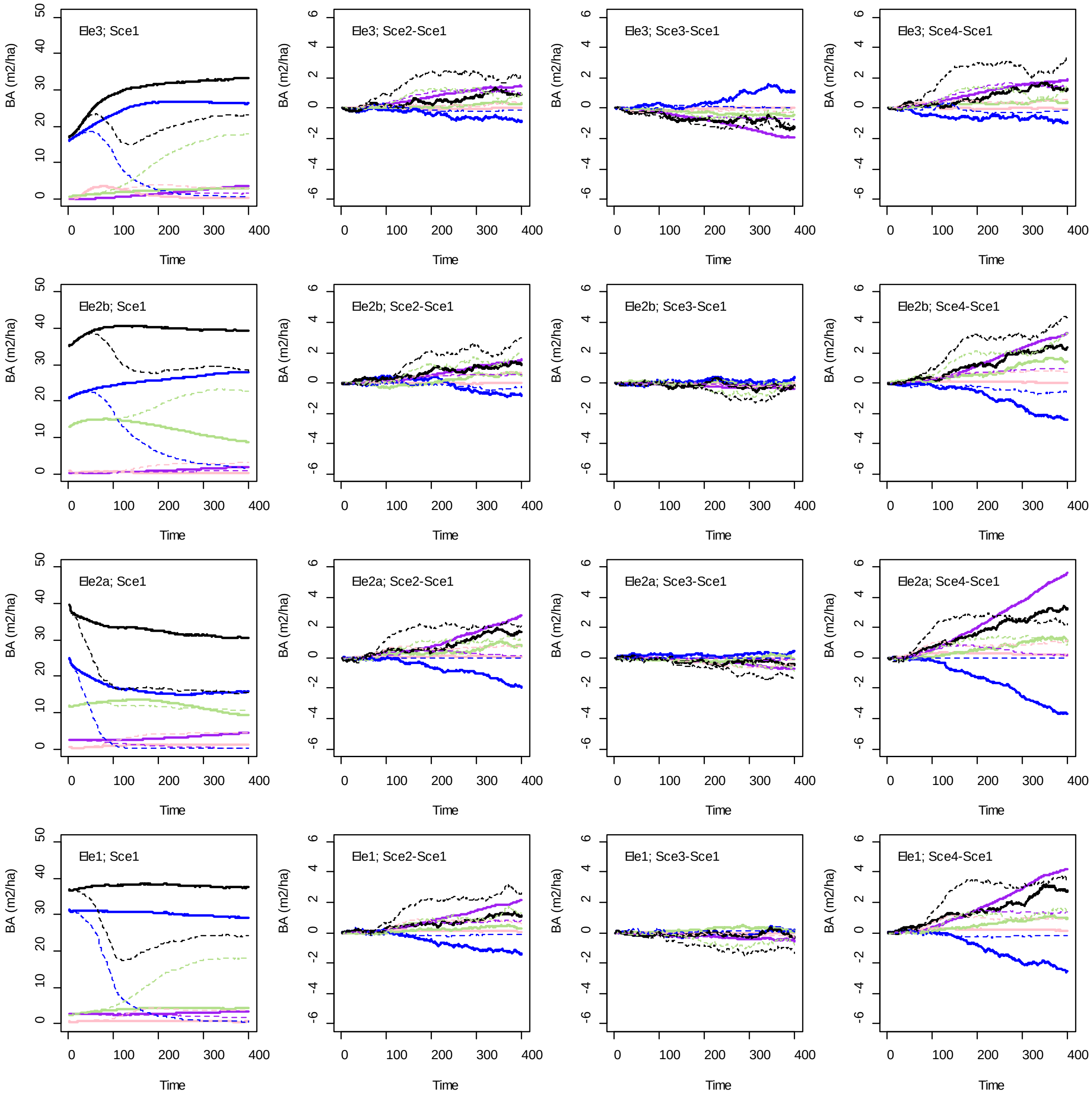

Initial state
Current climate
Climate change
3
2b
2a
1
P. abies
A. alba
F. sylvatica
others
Scen 1
Scen 2
Scen 3
Scen 4
Scen 1
Scen 2
Scen 3
Scen 4

Fig. 4



Ele3; Sce1
Ele3; Sce2-Sce1
Ele3; Sce3-Sce1
Ele3; Sce4-Sce1
Ele2b; Sce1
Ele2b; Sce2-Sce1
Ele2b; Sce3-Sce1
Ele2b; Sce4-Sce1
Ele2a; Sce1
Ele2a; Sce2-Sce1
Ele2a; Sce3-Sce1
Ele2a; Sce4-Sce1
Ele1; Sce1
Ele1; Sce2-Sce1
Ele1; Sce3-Sce1
Ele1; Sce4-Sce1
BA (m2/ha)
Time
0
100
200
300
400
0
10
20
30
40
50
-6
-4
-2
0
2
4
6

Fig. 5

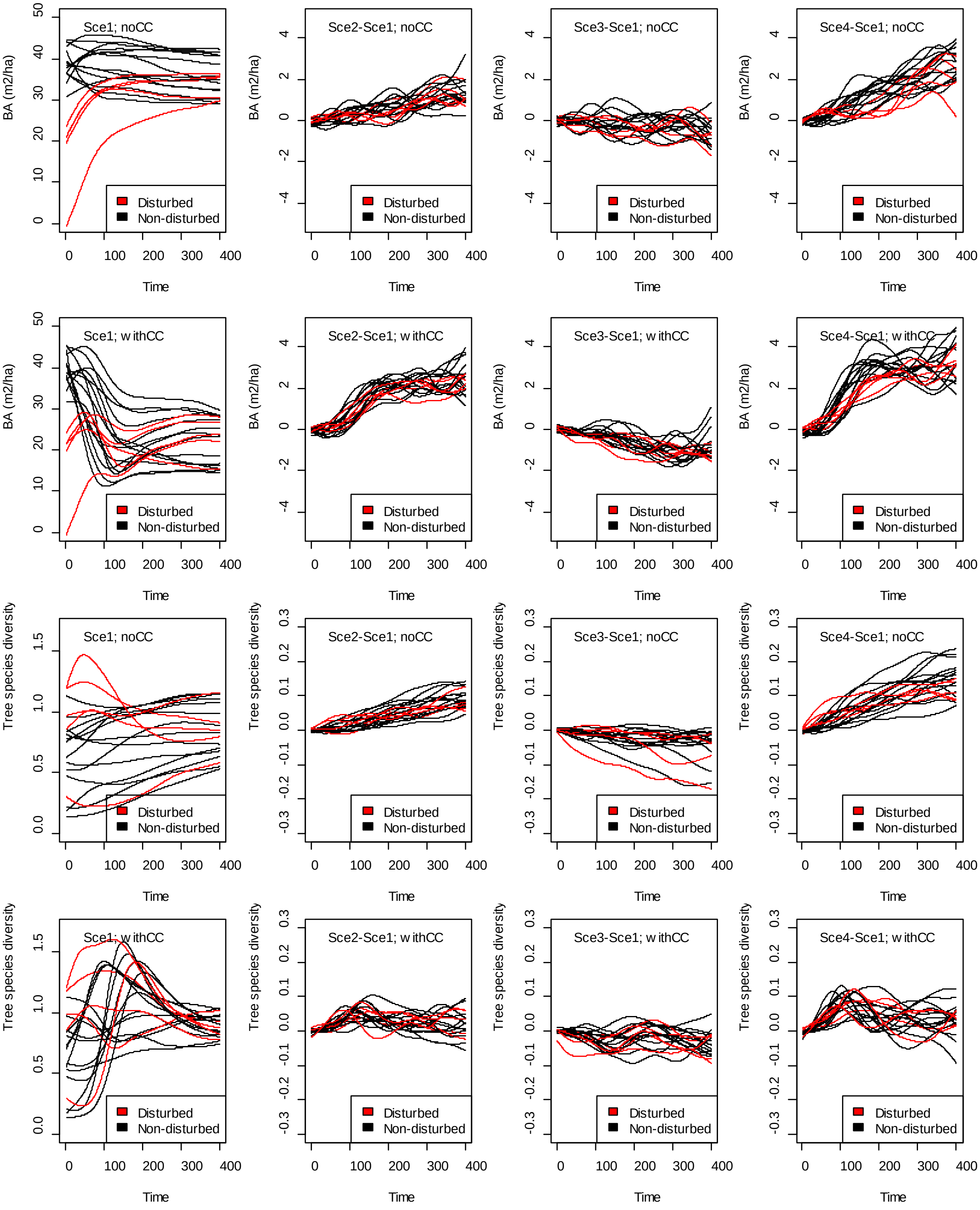

Sce1; noCC
Sce2-Sce1; noCC
Sce3-Sce1; noCC
Sce4-Sce1; noCC
Sce1; withCC
Sce2-Sce1; withCC
Sce3-Sce1; withCC
Sce4-Sce1; withCC
BA (m2/ha)
Tree species diversity
Time
0
100
200
300
400
0
10
20
30
40
50
-4
-2
0
2
4
0.0
0.5
1.0
1.5
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
🟥 Disturbed
■ Non-disturbed

Fig. 6

Appendix A: Climatic data

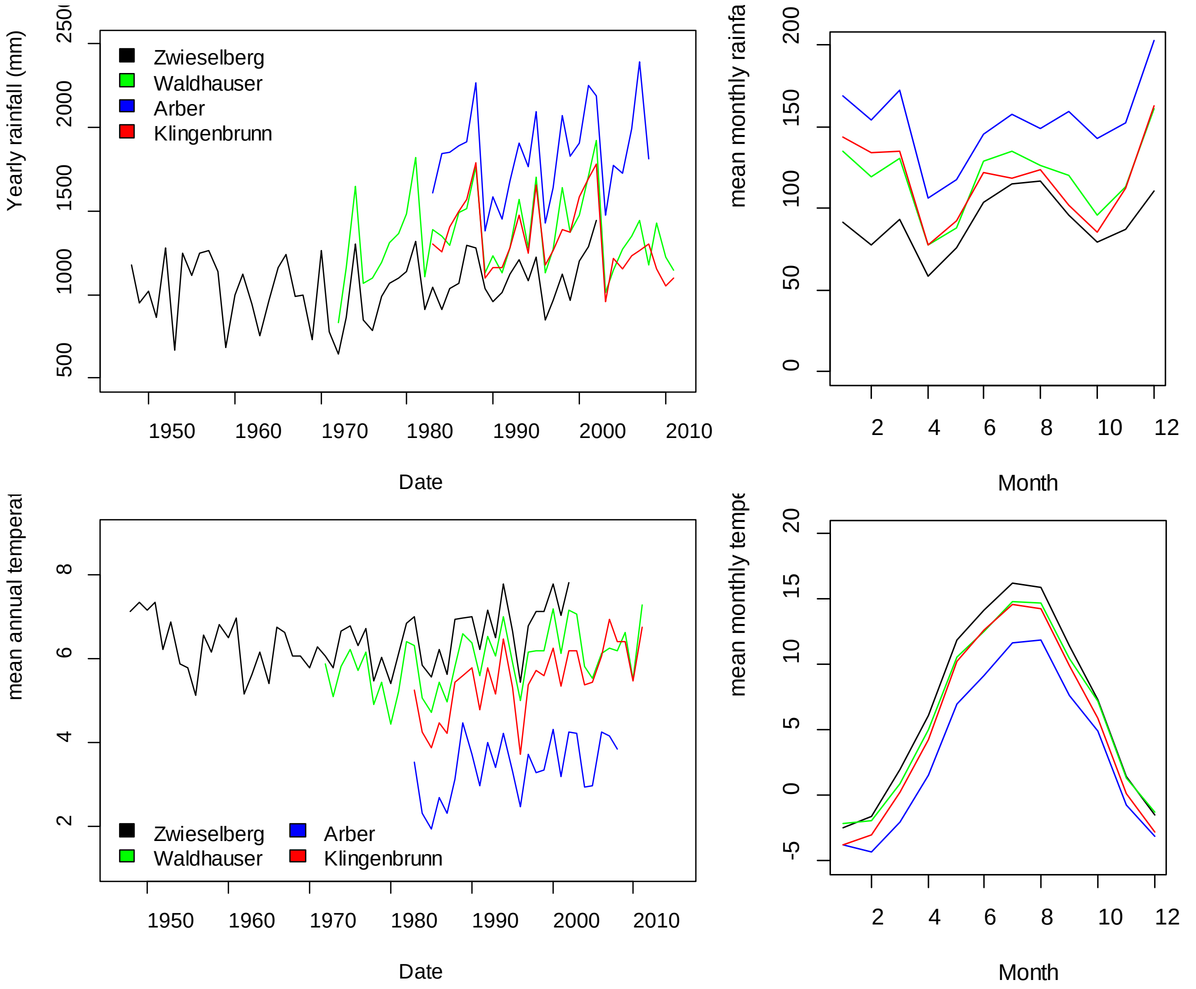


Fig. A1: Long-term changes (*Left*) and seasonal changes (*Right*; period 1983-2002) in rainfall (*up*) and mean temperature (*bottom*) on Zwieselberg (elevation: 615m a.s.l.) and three weather stations across the BFNP (Klingenbrunn: 756m, Waldhauser: 945m and Arber: 1437m).

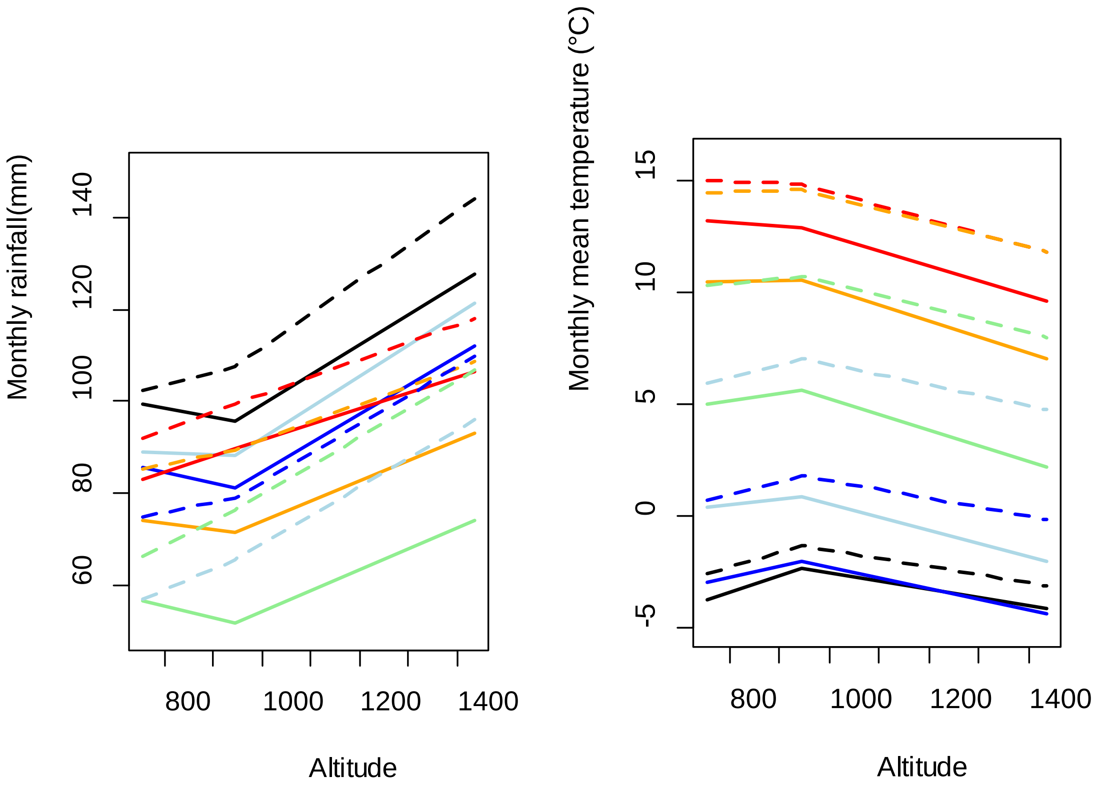


Fig. A2: Monthly altitudinal rainfall (*left*) and thermal (*right*) gradients between Klingenbrunn (756m), Waldhauser (945m) and Arber (1437m) for the period 1983-2002. January and December are indicated in black, February and November in dark blue, March and October in light blue, April and September in green, May and August in orange, and June and July in red. Since July, months are represented in dashed lines.

Table A1: Temperature (T) and rainfall (R) anomalies for the seasonal mean and the standard deviation of the seasonal mean for future state climate (2075-2100) compared with baseline (1961-2011) at the Zwieselberg weather station (scenario A1B normal). The predicted monthly cross-correlations (rTP) for the period 2075-2100 were also indicated.

Variable	Spring	Summer	Fall	Winter
Mean R (%)	-8.4	-21.9	-26.3	+37.7
Sd R (%)	-12.3	-6.3	-0.03	+23.7
Mean T (°C)	+0.92	+1.71	+1.87	+3.79
Sd T (°C)	-0.65	-0.34	-0.16	-0.08
rTP	-0.501	-0.362	-0.490	0.503

Appendix B: Clustering method used to define the different forest types (strata)

Choice of the model: Even if they are not widely used, hierarchical divisive clustering methods should be favored when analyzing forest inventory data as (i) the number of clusters is not predetermined such as for non-hierarchical techniques, and (ii) agglomerative methods strongly depend on the choice of the linkage method. As *k-means* tends to produce equi-sized clusters, which is hardly representative of reality, the Expectation-Maximization (EM) model approach was preferred as these models take advantage of the possibility of defining different Gaussian distributions among clusters (Banfield and Raftery 1993; Zhang et al. 2004). The best EM model (number of clusters; their orientation, shape and volume) was determined using the Bayesian Information Criterion (BIC; Schwarz 1978; Johnson and Omland 2004). To avoid the presence of clusters with few stands (*nbstands* < 60) which may be little representative of the studied area, we considered two further criteria for model selection: (i) the maximum number of clusters per topographic zone was set to 10, and (ii) the BIC of the model with *n* clusters must increase of at least 5% compared to the model with *n-1* clusters, otherwise the previous one was chosen.

Choice of the variables: For an easier biological interpretation of the clusters, the clustering analysis was made on raw data (after scaling and centering) instead of variables which derived from Principal Component Analysis. The abiotic component was already considered by differentiating the 4 topographic zones, consequently the cluster analysis is based on forest characteristics alone (biotic variables).

For each stand, trees with a height below 10 m (called *regeneration*) were separated from the taller ones (called *adult*). Dead trees were excluded from the analysis, which should allow for a classification of the stands according to the importance of bark beetle attacks.

We used the following variables:

- Stand basal area (BA) of adult trees is used to assess the developmental stage of the forest. Stand maximum DBH was not considered as the presence of few big trees may induce a high maximum DBH while BA is low.
- Percentage of adult spruce that died due to bark beetle or wind-throws (in number of trees).
- BA of the regeneration.

- As stands are mostly dominated by spruce, and also by beech at intermediate elevation, species composition was assessed using an index that depends on the percentages (of basal area) of both species, as follows: *IndexSpruceBeech = spruce percentage – beech percentage*. It thus ranged between -1 and 1, where negative values indicate a stand dominated by beech, and positive ones dominance by spruce. Zero was obtained either when there were no trees, or when spruce basal area equaled the one of beech. Even if it doesn't reveal the percentage of the other species, this index seems appropriate in this area with low tree species diversity. This *IndexSpruceBeech* was calculated for both adult and regeneration stages.

All these clustering analyses were performed using the *mclust* package in R (Fraley et al. 2012).

Table B1: Averaged altitude of each zone [95% Confidence interval], and main characteristics of the best mixture models (VEV= ellipsoidal, equal shape; EEV= ellipsoidal, equal volume and equal shape; df= degrees of freedom; BIC= Bayesian Information Criterion)

Zone	Nb stands	Altitude [CI]	Exposure [CI]	Slope [CI]	model	df	BIC	Nb clusters
Low elevation (1)	922	776 m [649-954]	175 [169-180]	4.7 [4.5-4.9]	VEV	71	-7712.0	4
Bottom of the slopes (2a)	1850	830 m [631-1062]	199 [195-203]	9.5 [9.3-9.6]	EEV	100	-17557.3	6
Top of the slopes (2b)	2103	1038 m [860-1240]	192 [188-195]	13.1 [12.9-13.3]	VEV	88	-17008.4	5
High elevation (3)	930	1192 m [1009-1342]	181.4 [175-188]	9.9 [9.6-10.3]	EEV	68	-6829.0	4

Please follow this legend for the following figures (**Figs. B1 - B4**).

🟪 Abi. alb.
🟦 Lar. dec.
🟦 L. Pic. Abi.
⬜ D. Pic. Abi.
🟨 Pin. Mon.
⬜ Tax. Bac.
🟪 Acer Pla.
🟧 Aln. Glu.
🟧 Aln. Inc.
⬜ Bet. Pen.
🟥 Fra. Exc.
🟩 Fag. Syl.
🟥 Pop. Nig.
🟥 Pop. Tre.
🟩 Que. Rob.
⬜ Sal. Alb.
🟦 Sor. Auc.
🟨 Til. Cor.
🟨 Til. Pla.
🟧 Ulm. Gla.
⬛ others

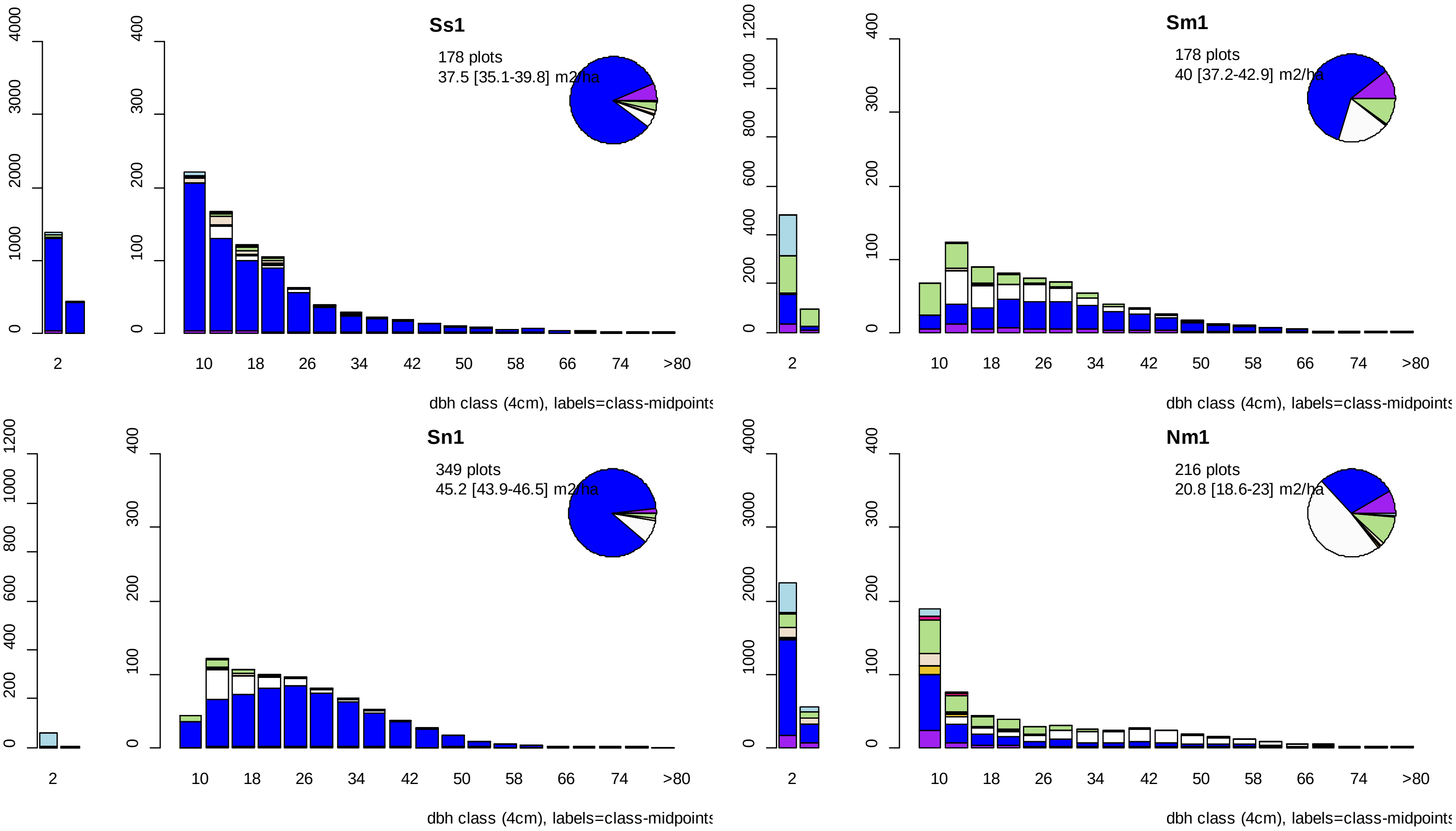
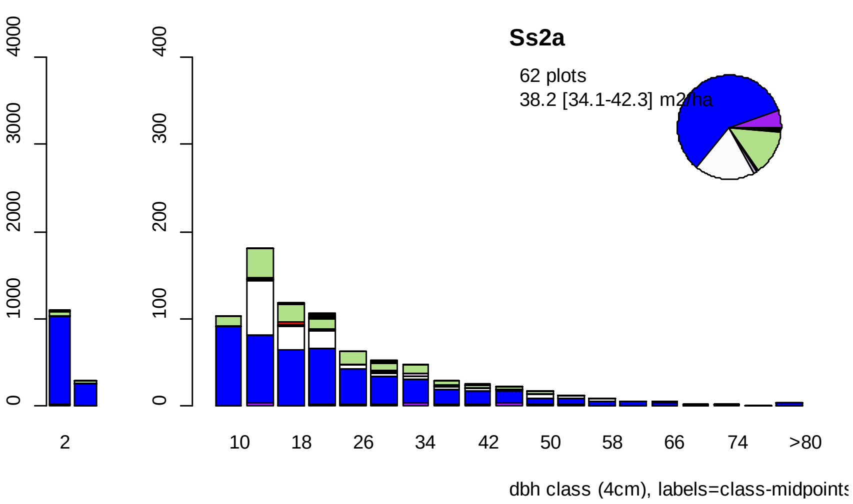
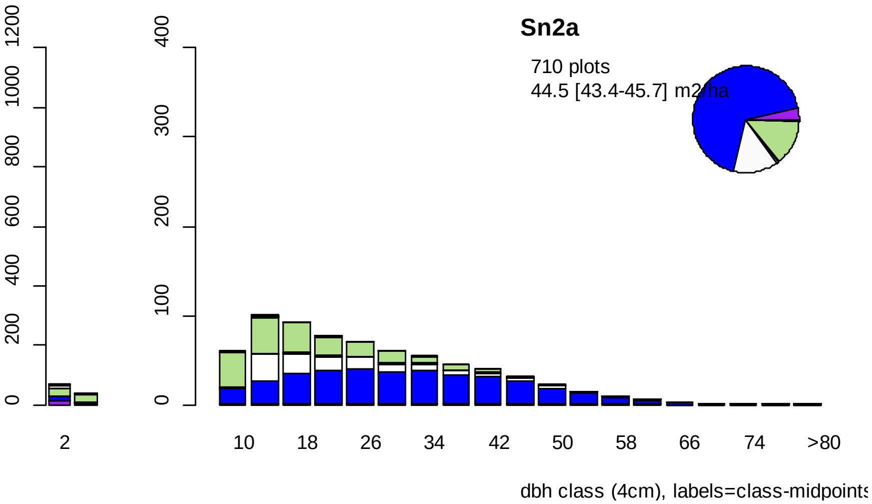
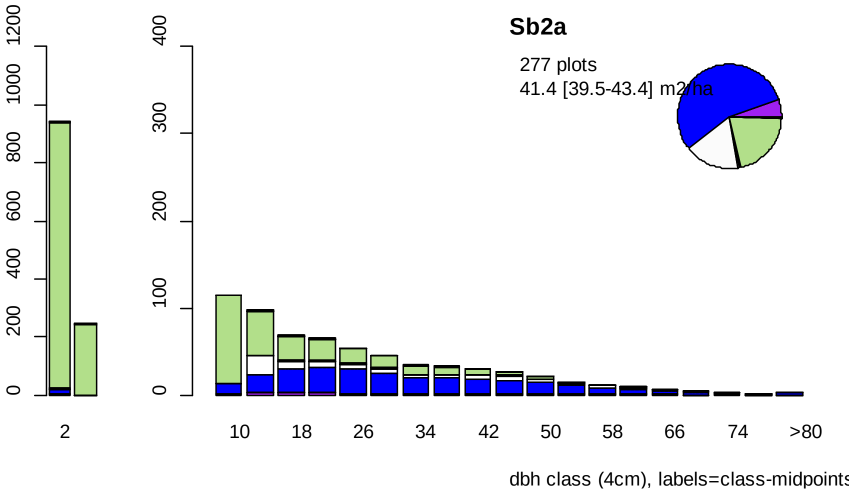
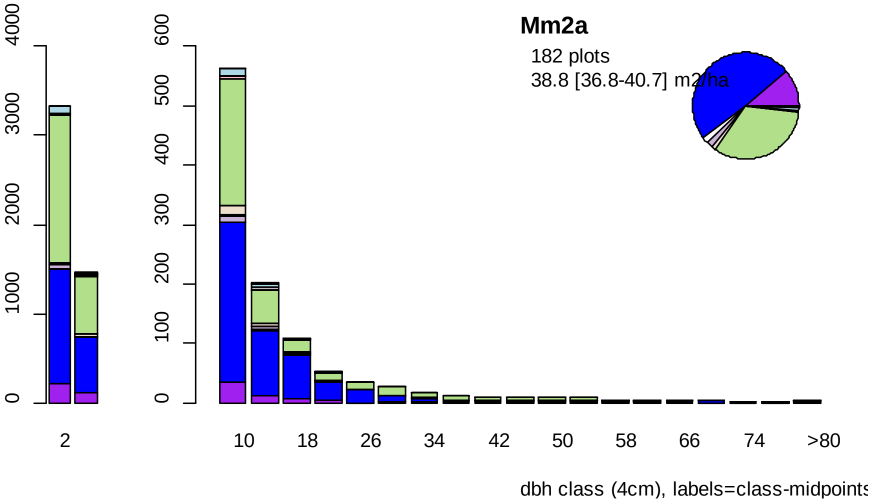


Fig. B1: Diameter distribution (number of trees per hectare) of the main strata defined by cluster analysis for **Low elevation** stands. For each stratum the number of stands, the mean and confidence interval (95%, in brackets) of basal area of living trees are also indicated, as well as the proportion of each species in the stand basal area (pie graph).


Ss2a
62 plots
38.2 [34.1-42.3] m2/ha
0
1000
2000
3000
4000
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Sn2a
710 plots
44.5 [43.4-45.7] m2/ha
0
200
400
600
800
1000
1200
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Sb2a
277 plots
41.4 [39.5-43.4] m2/ha
0
200
400
600
800
1000
1200
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Mm2a
182 plots
38.8 [36.8-40.7] m2/ha
0
1000
2000
3000
4000
2
0
100
200
300
400
500
600
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints

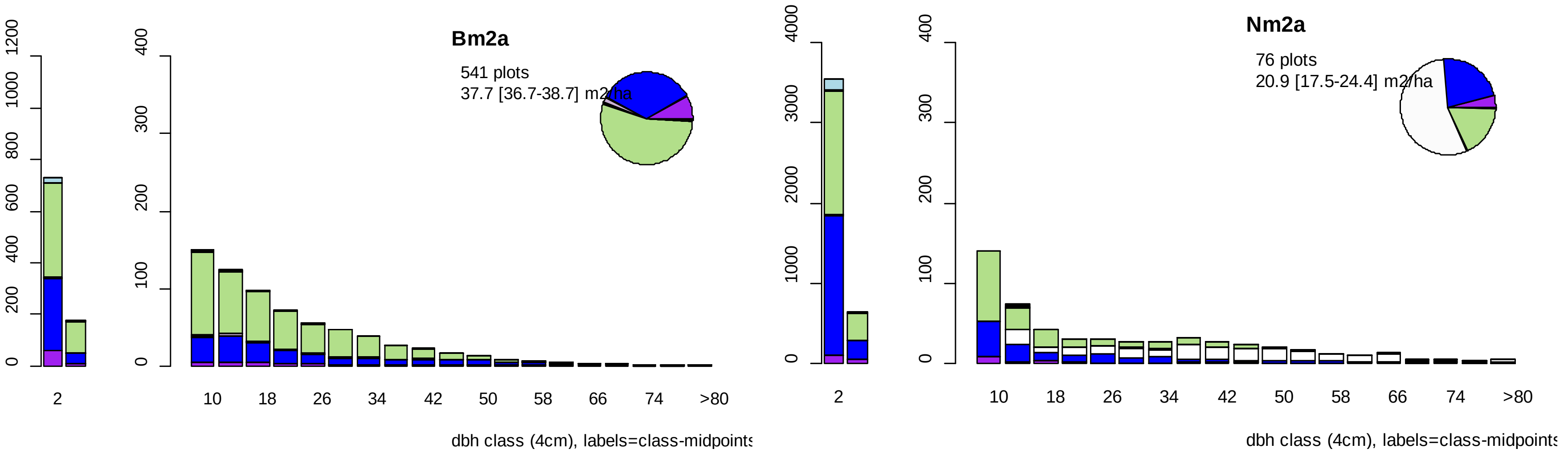
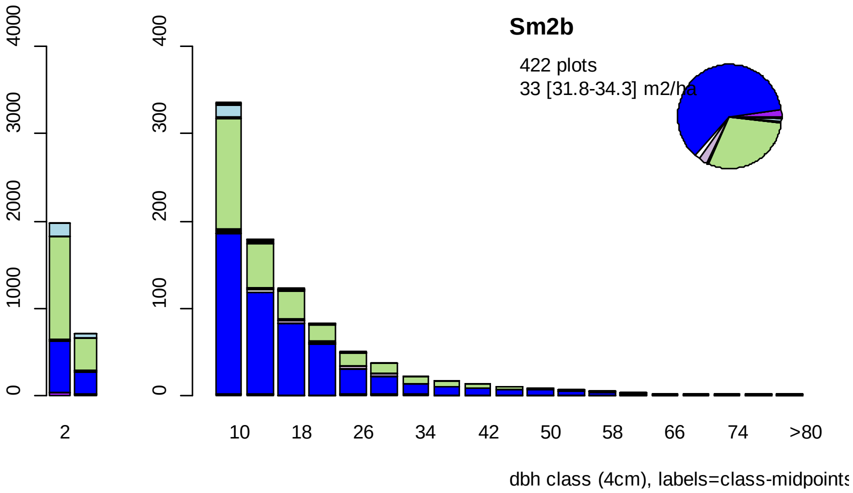
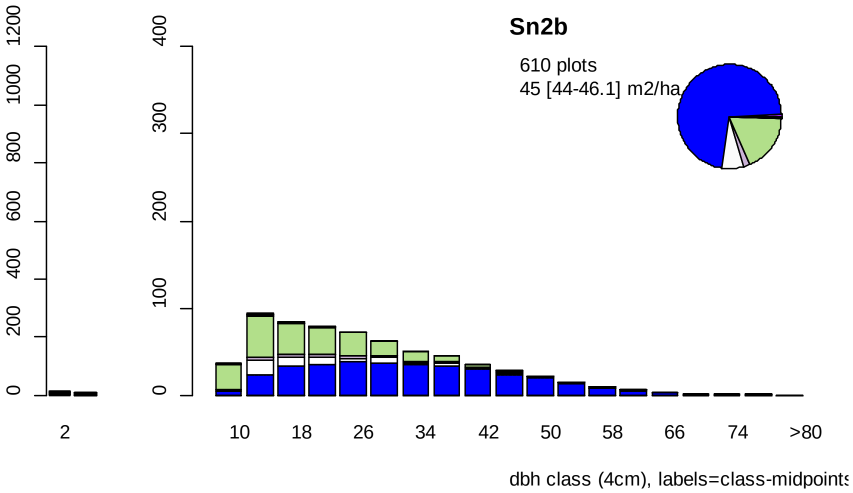
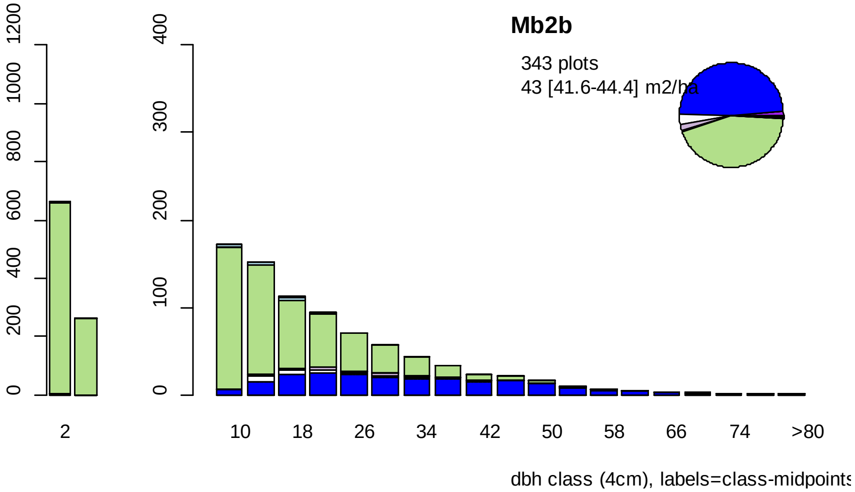
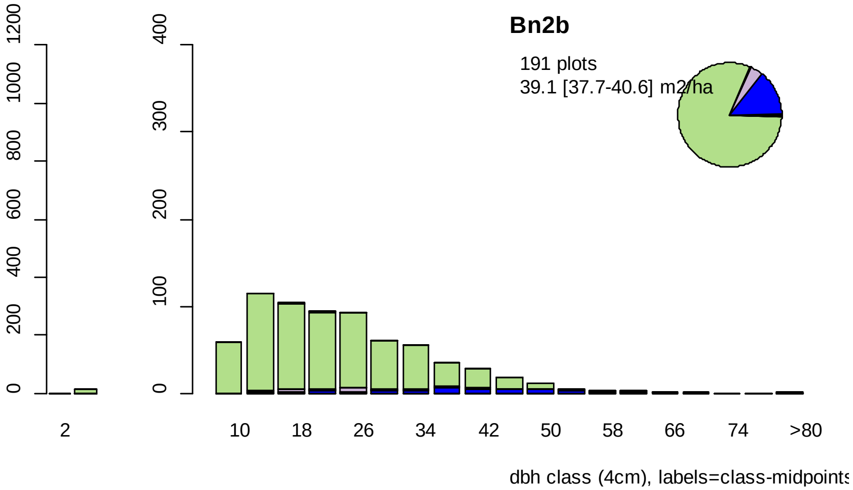


Fig. B2: Diameter distribution (number of trees per hectare) of the main strata defined by cluster analysis for the stands located at the **Bottom of the slopes**. For each stratum the number of stands, the mean and confidence interval (95%, in brackets) of basal area of living trees are also indicated, as well as the proportion of each species in the stand basal area (pie graph).


Sm2b
422 plots
33 [31.8-34.3] m2/ha
0
1000
2000
3000
4000
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Sn2b
610 plots
45 [44-46.1] m2/ha
0
200
400
600
800
1000
1200
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Mb2b
343 plots
43 [41.6-44.4] m2/ha
0
200
400
600
800
1000
1200
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints


Bn2b
191 plots
39.1 [37.7-40.6] m2/ha
0
200
400
600
800
1000
1200
2
0
100
200
300
400
10
18
26
34
42
50
58
66
74
>80
dbh class (4cm), labels=class-midpoints

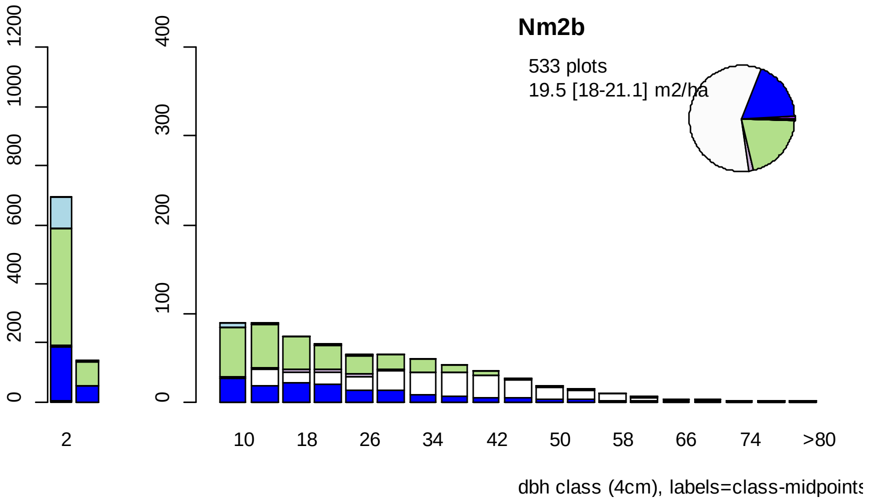


Fig. B3: Diameter distribution (number of trees per hectare) of the main strata defined by cluster analysis for the stands located at the **Top of the slopes**. For each stratum the number of stands, the mean and confidence interval (95%, in brackets) of basal area of living trees are also indicated, as well as the proportion of each species in the stand basal area (pie graph).

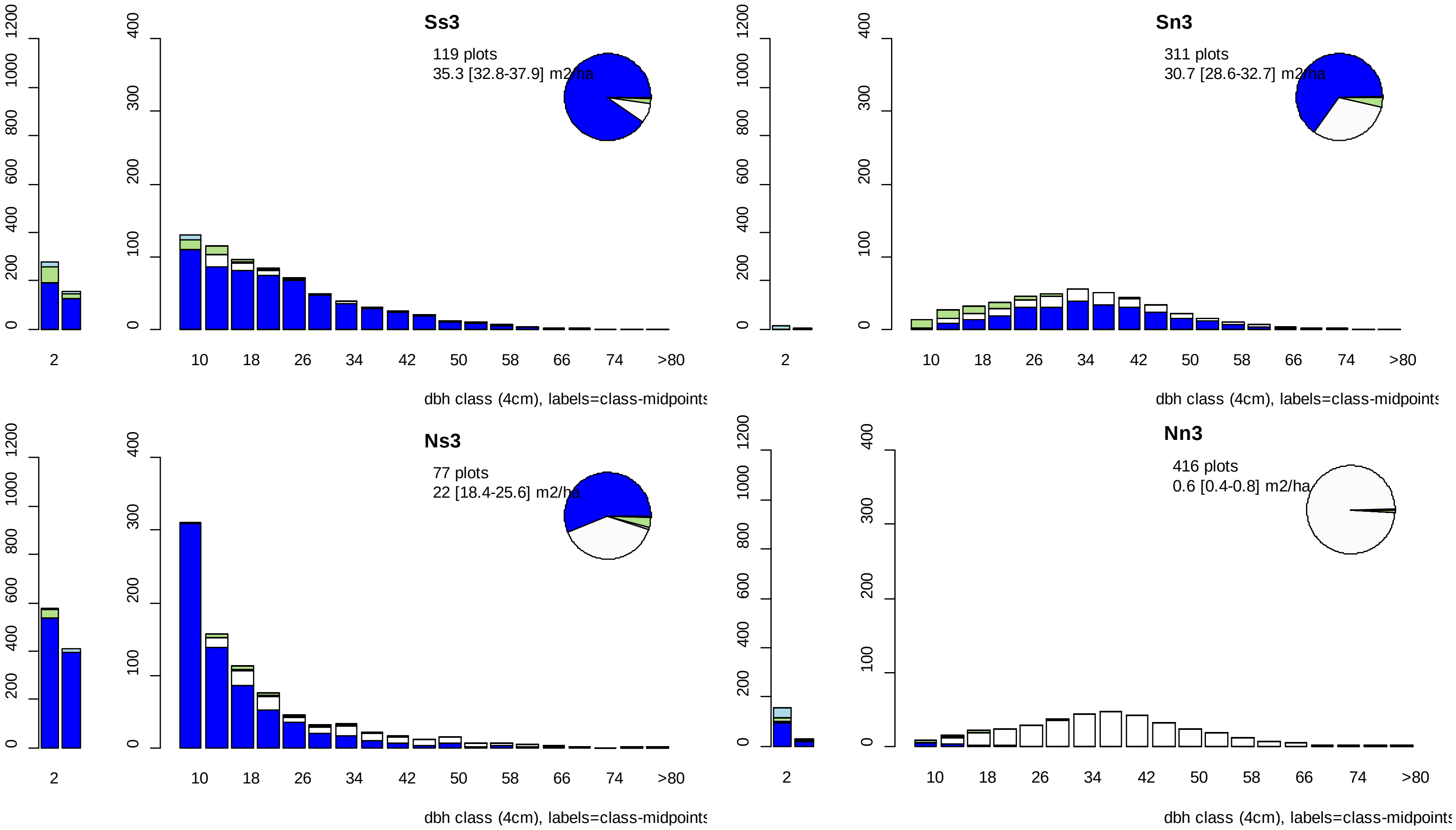


Fig. B4: Diameter distribution (number of trees per hectare) of the main strata defined by cluster analysis for **High Elevation** stands. For each stratum the number of stands, the mean and confidence interval (95%, in brackets) of basal area of living trees are also indicated, as well as the proportion of each species in the stand basal area (pie graph).

Appendix C: Fit of the beta distributions to assess the frequency of browsing probability for each tree species

The variability in browsing probability among stands has been quantified for each species by fitting beta distributions on the frequency of browsing probability calculated for the whole BFNP. In each case we removed stands where the species of interest has not been observed in the seedling bank. Beta distributions were fitted according to the “matching moment estimation” method using the package fitdistrplus (Delignette-Muller et al. 2012).

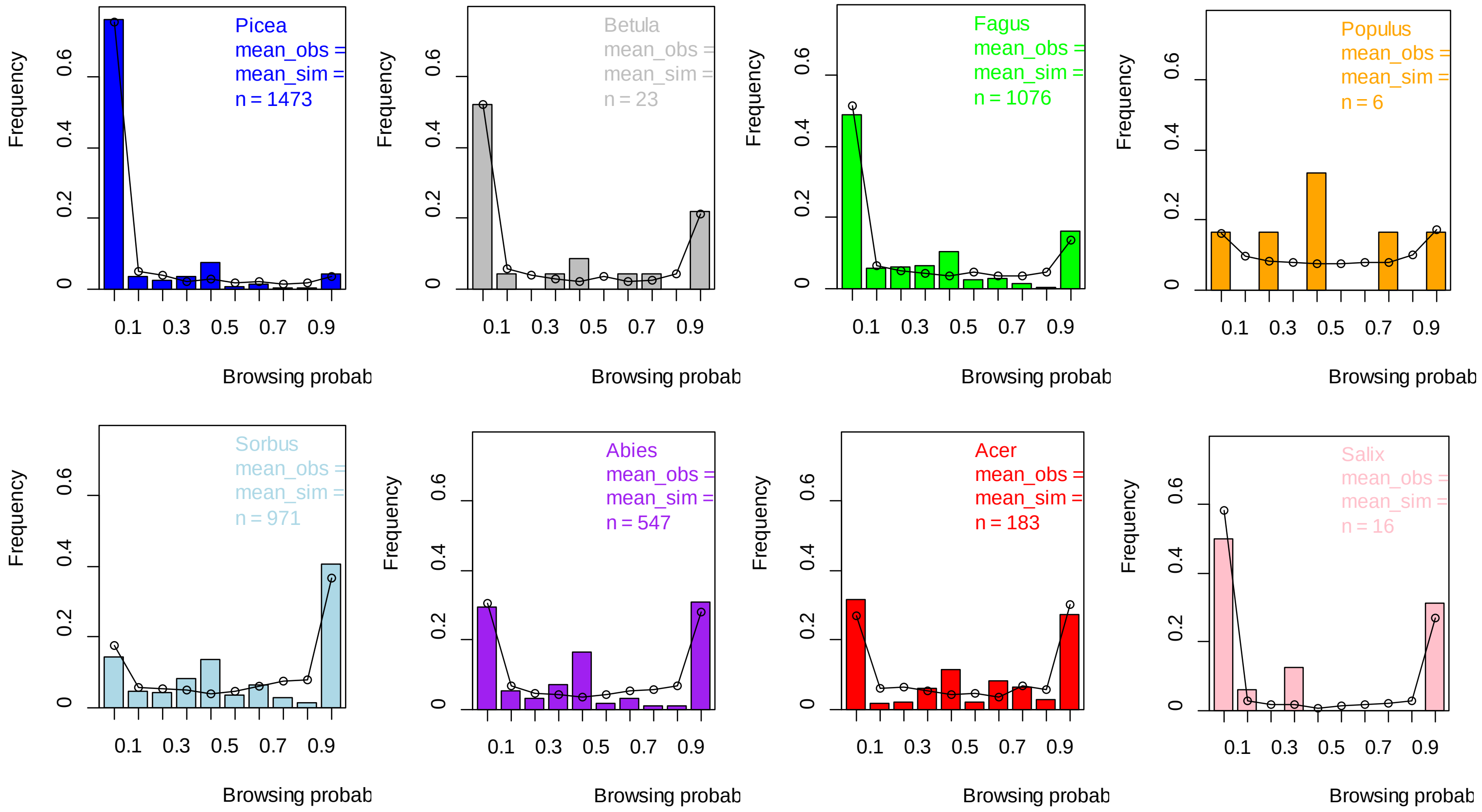


Fig. C1: Frequency of browsing probability among stands for each main species of the BFNP (bars). Black circles and lines indicate the best beta distribution defined using the “matching moment estimation” method. Parameters of these beta distributions were used to fit linear regressions of **Fig. 2** of the manuscript. For each species the average browsing probability observed in the field and calculated using the beta distribution (sim; 5000 iterations) were also indicated.

Aggregation of these distributions at larger spatial scale

As these beta distributions were fitted for $25m^2$ stands, we had to aggregate the data at larger spatial scale to assess browsing probability variability at $500m^2$ scale (minimum size of a patch for ForClim simulations). To this aim, we choose 20 random numbers within the beta function to obtain a mean browsing probability at $500m^2$ scale. We obtained normal distributions of species-specific browsing probability at stand scale ($kBrP_s$) whose mean and standard deviation depend on species preference by ungulates (BPU; **Fig. C2** *Right*).

Unfortunately this spatial aggregation approach was likely unrealistic as the spatial correlation of $kBrP_s$ among the twenty $25m^2$ plots within the $500m^2$ patch was not considered (if $kBrP_s$ in one plot equals 1, $kBrP_s$ of the surroundings plots is probably closer to 1 than to 0). Numbers within the beta distribution shouldn't be randomly chosen, but our browsing survey didn't allow us to quantify this spatial correlation of $kBrP_s$ between $25m^2$ plots.

In consequence, we did a sensitivity analysis to test the impact of different spatial aggregation of $kBrP_s$ on forest dynamics simulated by ForClim with 3 different cases:

- $kBrP_s$ is randomly chosen within the beta function (equivalent variability of $kBrP_s$ at $500m^2$ than at $25m^2$)
- 2 numbers are randomly chosen within the beta function and averaged to obtain $kBrP_s$ (equivalent variability of $kBrP_s$ at $500m^2$ than at $100m^2$; **Fig. C2** *Middle*)
- 20 numbers are randomly chosen within the beta function and averaged to obtain $kBrP_s$ (spatial aggregation without any consideration of the spatial correlation of $kBrP_s$; **Fig. C2** *Right*)

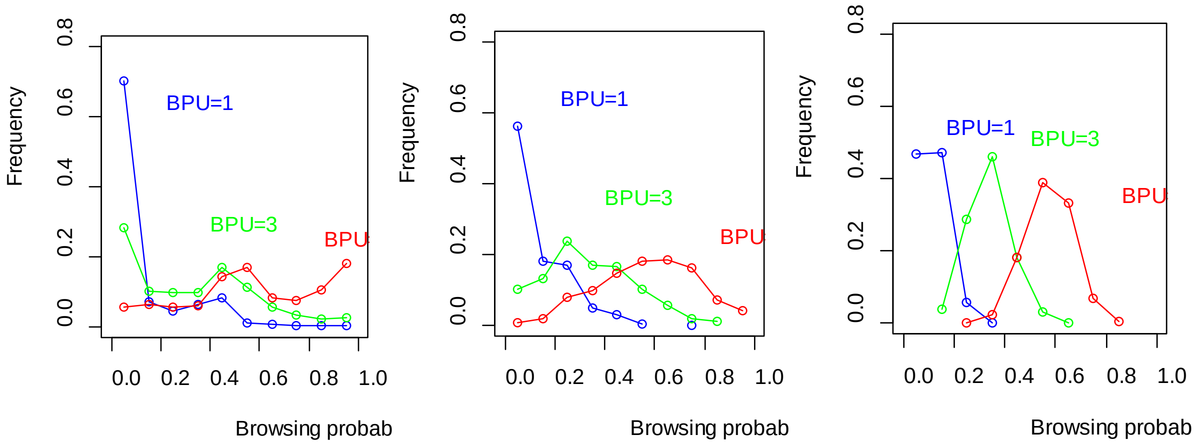


Fig. C2: Effect of patch size on the frequency of browsing probability among patches. Respectively 1, 2 and 20 numbers were randomly chosen within the beta distribution were averaged to obtain a mean browsing probability in a 25 m^2 *(Left)*, 50 m^2 (*Middle*) and 500 m^2 *(Right)* patch. 1000 samples per patch size were used for calculating these frequencies.

Effect of the aggregation scale on browsing probability establishment flag (BPEF) and on forest properties simulated by ForClim.

The aggregation scale used for calculating $kBrP_s$ differently impacted species BPEF according to their preference by ungulates (BPU) and sensitivity to browsing (kbrow parameter; **Fig. C3** *Left*). If the quantity of numbers chosen within the beta distribution increased, from 1 to 2 or from 1 to 20, spruce BPEF decreased while silver fir BPEF increased and beech BPEF remained constant. This species-specific effect of the aggregation scale was due to the non-linear relationship between browsing probability ($kBrP_s$) and the mortality probability due to browsing ($kMorBrP_s$; **equation 5** in the manuscript; from Didion et al. 2011). For *A. alba*, mean $kMorBrP_s$ was more dependent on changes in $kBrP_s$ frequency within the range [0 – 0.2] than within the range [0.8 – 1]. In consequence, averaging $kBrP_s$ values, which induced a reduction in the frequency of $kBrP_s$ within both ranges (**Fig. C2**), led to an increase in $kMorBrP_s$ (**Fig. C3** *Left*).

However, forest properties were slightly impacted by this conceptual change. In comparison to the reference run (aggregation scale equals 25m^2), there were no significant changes after 100 years of simulation whatever the species and the browsing scenario (**Fig. C3** *Middle* and **Table C1**; the significant effect of the interaction species * scenario was not relevant). At PNV, the model predicted a decrease in *A. alba* BA and an increase in *P. abies* BA while *F. sylvatica* was not affected by this change **(Table C1; Fig. C3** ***Right*****)**. These species-specific responses were dependent to the aggregation scale as the differences to the reference run were larger with an aggregation scale of 500m^2 than with 50m^2 (**Table C1**). The decrease in *A. alba* BA was respectively in the order of -1m^2/ha and -0.6m^2/ha and the increase in *P. abies* BA of 0.75m^2/ha and 0.52m^2/ha. These differences in BA were especially strong when the browsing intensity is low (**Table C1**) but did not exceed -2m^2/ha or +2m^2/ha (**Fig. C3** *Right*).

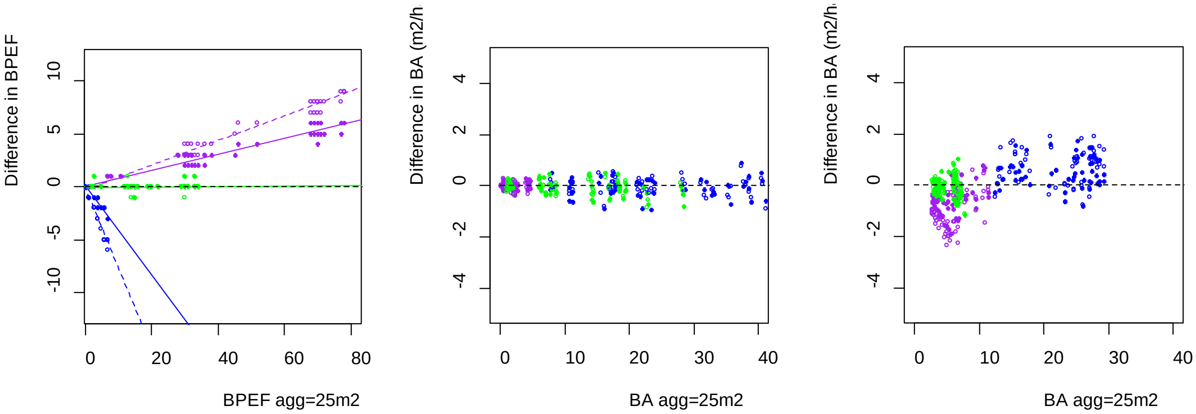


Fig. C3: Effect of the aggregation parameter on the difference in BPEF (*Left*) and in BA (*Middle* after 100 years of simulation; *Right* at PNV [2000 years]) for *P. abies* (blue), *F. sylvatica* (green) and *A. alba* (purple) of each stratum (circles). Closed and empty circles respectively represented the difference in BPEF and BA calculated with an aggregation scale of 50m^2 (average of 2 numbers within the beta distribution) and 500m^2 (average of 20 numbers) in comparison with the reference run (25m^2, 1 number). Simulations were done using the browsing scenarios 1, 2 and 3 and under current climate.

Variable	Df	T=100 years			T=2000 years (PNV)		
		Sum Sq	F value	P-value	Sum Sq	F value	P-value
species	2	0.2	1.6		**117.2**	**238.8**	**<0.001**
aggregation	1	0.0	0.0		0.1	0.4	
Browsing scen	2	0.2	1.9		0.4	0.7	
BA init	1	0.0	0.0		**1.9**	**7.7**	**<0.01**
sp * agg	2	0.2	1.4		**4.8**	**9.9**	**<0.001**
sp * browsing	4	**1.9**	**7.7**	**<0.001**	**26.7**	**27.2**	**<0.001**
sp * BA init	2	0.1	0.5		1.0	2.0	
agg * browsing	2	0.0	0.3		0.1	0.1	
agg * BA init	1	0.2	3.3	<0.1	0.1	0.5	
browsing* BA init	2	0.0	0.1		0.4	0.7	
Residuals	322	20.1			79.0		

Table C1: Results of analysis of variance for the difference in BA simulated with both 50m^2 and 500m^2 aggregation scales and predicted by the reference run (aggregation scale=25m^2).

Appendix D: Implementation of a seedling bank into ForClim establishment submodel

In order to obtain a total number of seedlings close to reality and relevant spatio-temporal variability in ungulates presence probability, we had to define a maximum number of seedlings per species per hectare. After some tests we decided to fix this maximum at 500 seedlings per species per hectare although the observed and simulated distributions of the number of seedlings per stand strongly differ (**Fig. D1**). Firstly, the current functioning of the seedling bank in ForClim (**eq. 1** in the manuscript) cannot reconstruct such observed log-normal distribution with many stands without seedlings and few stands with a very large number of seedlings (until 500000 seedlings.ha^{-1}). Indeed seedling establishment of shade-tolerant species such as *A. alba* is always possible even under dense canopy (**Fig. D2**), and the maximum number of seedlings that can establish in a modelling framework cannot be unlimited. Secondly, this log-normal distribution determined using field data is probably not comparable of the real one. On each stand, the observed number of seedlings per hectare was determined by extrapolating the number of seedlings reported on a 25m^2 scale, and should be not representative of the real the number of seedlings reported on one hectare.

The current functioning of seedling bank overestimates the average number of seedlings per hectare (**Fig. D1**) and, in consequence, the probability of ungulates presence on the stands (**Table 2**). However this bias was similar for each studied stratum and didn't influence the spatial and temporal variability in ungulates presence probability that seemed to be realistic (**Fig. D3 and Fig. D2**).

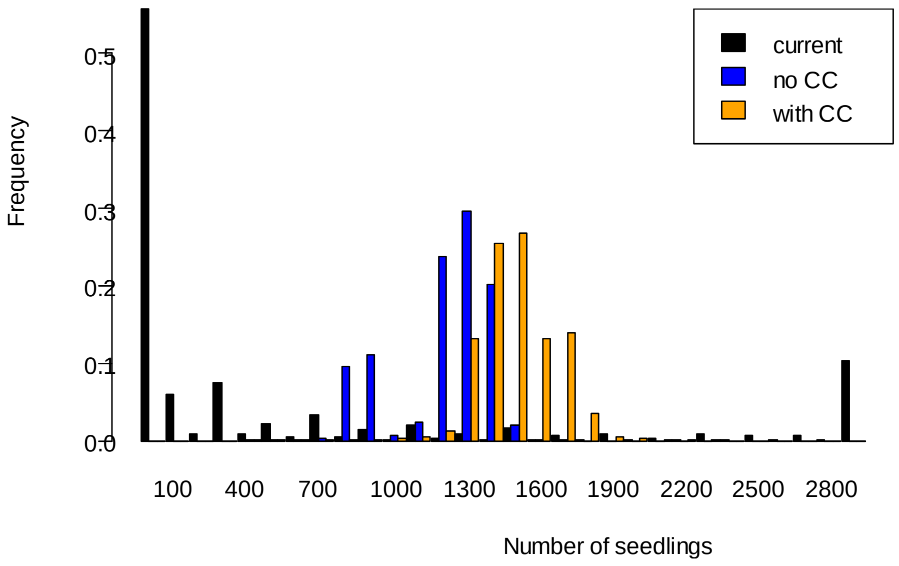


Fig. D1: Distribution of the number of seedlings per hectare observed in each stand (current state; black) and simulated by ForClim during 2000 years (4 browsing scenarios * 3 aggregation scenarios) considering climate change (orange) or not (blue). If we consider all the stands, the average number of seedlings per stand respectively approximated 970 and 2245 for simulated and observed data (median=0 and 0), while if we remove the stands without seedlings it approximated 2010 and 6700 (median=800 and 1600).

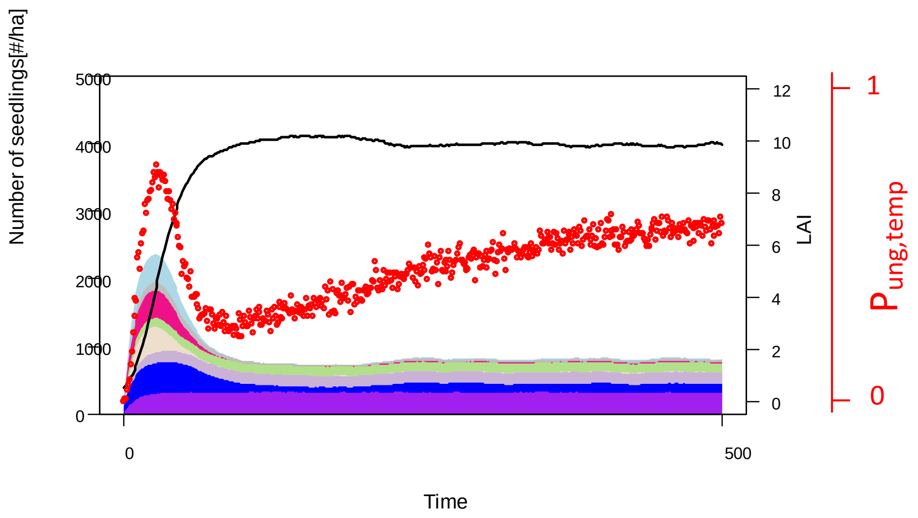


Fig. D2: Evolution across time of the number of seedlings of each species (legend in Appendix B), of double-sided Leaf Area Index (black line), and quantitative ungulates presence probability ($P_{ung,temp}$, red circles) at the stratum *Nn3* for the averaged browsing intensity (scenario 1).

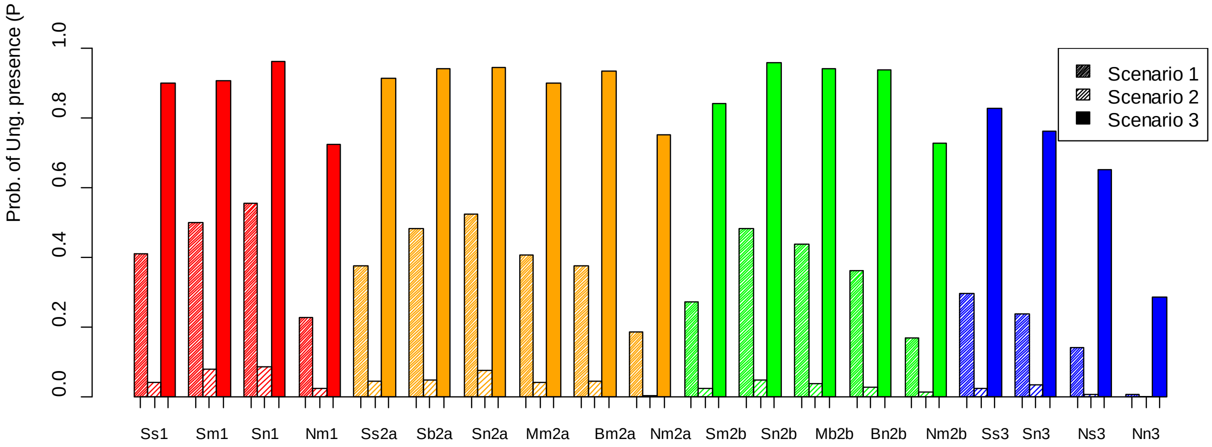


Fig. D3: Probability of ungulates presence averaged across 400 years of simulation for each stratum and for the three main browsing scenarios. Low elevation stands are colored in red, stands located at the bottom and top of the slopes in orange and green, and high elevation stands are in blue.

The inclusion of a seedling bank in ForClim strongly impacted short-term simulations (**Fig. D4**). The new version favored spruce and beech establishment thanks to the change in the calculation of the annual probability of tree establishment ($gPest_s$ is not directly impacted by climatic conditions anymore and is now less variable). This induced an increase in trees number and basal area (BA) of both species at short-term (0-400 years) and changed environmental conditions that began more and more favorable for silver fir establishment.

That could be due to the effect of the initialized seedling bank on tree establishment. However results were almost the same when simulations were run with a seedling bank initialized by simulating inputs of seedlings from 10 years with variable climatic conditions and same light conditions (data not shown). This indicated that the change in trees number and BA was really due to the creation of the seedling bank and not to its initialization using a state file.

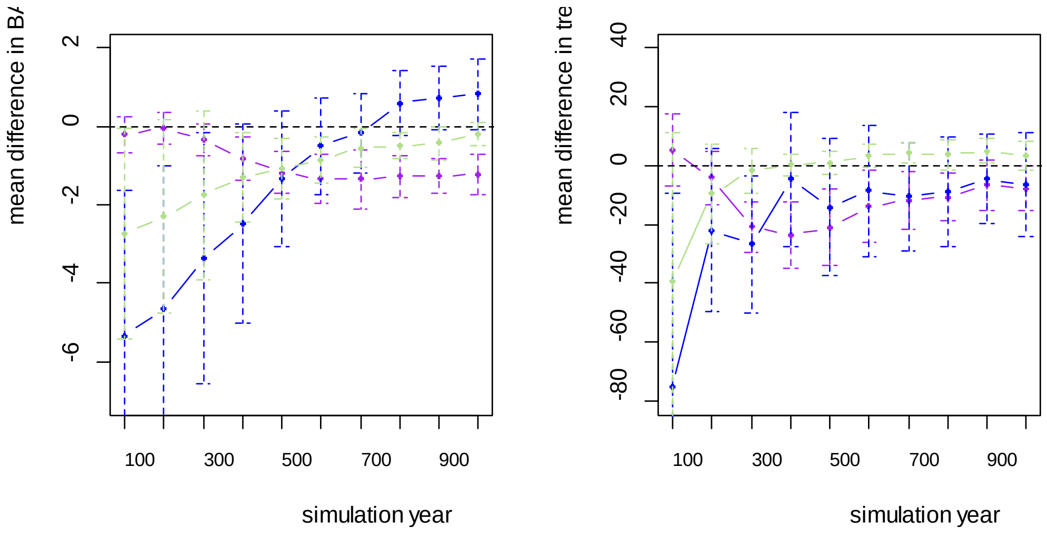


Fig. D4: Changes over time of the difference in stand BA (*Left*) and number of trees (*Right*) simulated by previous ForClim version and ForClim with seedling bank. Simulations were done using current climatic conditions and without browsing. The results were only represented for the main species: *P. abies* (blue), *F. sylvatica* (green) and *A. alba* (purple).

Appendix E: Assessment of the best threshold used to determine the probability of ungulates presence (P_{ung}, binary variable) according to $P_{ung,temp}$ (continuous variable ranging between 0 and 1)

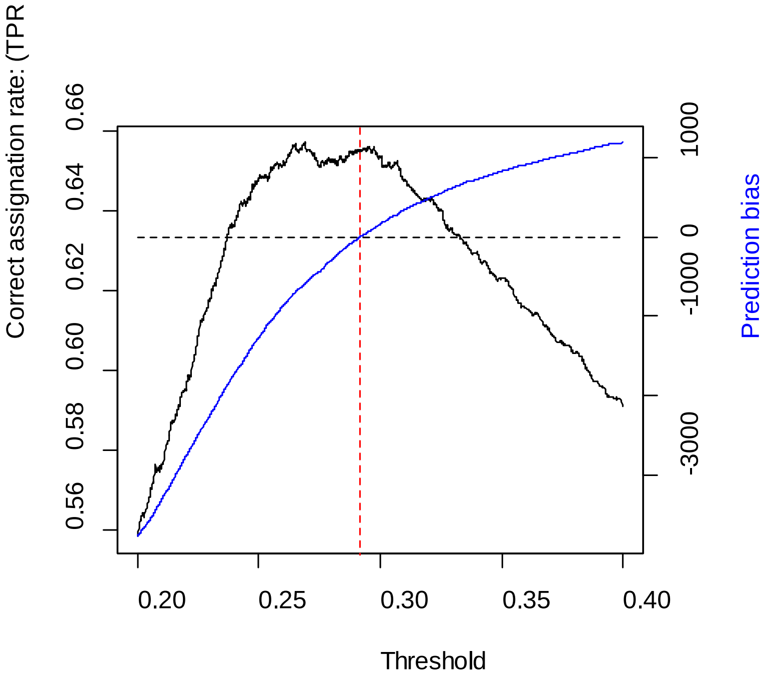


Fig. E1: Correct classification rate (average of the True Positive Rate and True Negative Rate; black) and prediction bias (number of presence observed – number of presence simulated; in blue) for different threshold values. Negative prediction bias indicates an overestimation of ungulates presence. No bias at threshold = 0.2919 where CCR = 0.665, TPR = 0.505, and TNR = 0.806.

Appendix F: ForClim sensitivity to the number of patches per stratum used to simulate forest dynamics

To reduce the stochastic ‘noise’ in the simulation results, Bugmann et al. (1996) suggested to perform simulations with *nbruns* = 200 patches (500 m^2 size). For the present study, however, the best number of simulated patches may differ because (i) the forest simulation did not start from bare ground but was initialized with empirical stand data, and (ii) the number of stands used for initialization differed between each stratum.

In consequence, the best number of patches used for the simulation of each stratum was tested by comparing different simulation sets:

- In the first set, as the highest number of plots within a stratum equals 712 (*Sn2a*), simulations were performed with 750 different patches for each stratum. This simulation set should include low stochastic ‘noise’ and thus will be considered as the reference in the following analyses.
- We also run simulations with *nbruns* = 200 and 400 patches that may be preferred to avoid long simulation times.
- Finally, we considered that each stand of the stratum equals one patch in ForClim (from 62 to 712; see **Table 1**).

For simulations with a constant *nbruns*, each plot was replicated if necessary (if the number of stands per stratum is below *nbruns* / 2), and the remaining number of patches was randomly sampled without replacement within all plots of the stratum.

We compared the resulting difference in terms of number of trees [N; $trees.ha^{-1}$] and of basal area [BA; $m^2.ha^{-1}$] at different simulation times and for each stratum. Simulations were done without browsing and climate change.

The use of 200, 400 or a variable number of patches didn’t significantly change mean N and BA calculated across all strata whatever the simulation year (**Fig. F1**). However these differences were not negligible at the scale of one stratum especially for strata with low number of stands (**Fig. F2**). With a variable *nbruns*, the change in stand BA after 100 years of simulation could exceed $5m^2/ha$, for instance the model simulated a decrease in 18% of BA ($-6.9/37.3\ m^2.ha^{-1}$) at the stratum *Ns3* and in 7% of N (-96/1358 trees.ha^{-1}) at the stratum *Ss2a* which respectively included 77 and 62 plots only. The lowest differences in N and BA were obtained for *nbruns*=400. Similarly differences in species N proportion were the lowest for *nbruns*=400 (**Fig. F3**) while can be significant at some stands when using a variable nbruns (*e.g.* in *Ss2a*: p<0.05 at t=600 years and p<0.001 at t=1000 years)

For these reasons, simulations were performed with *nbruns* = 400 patches.

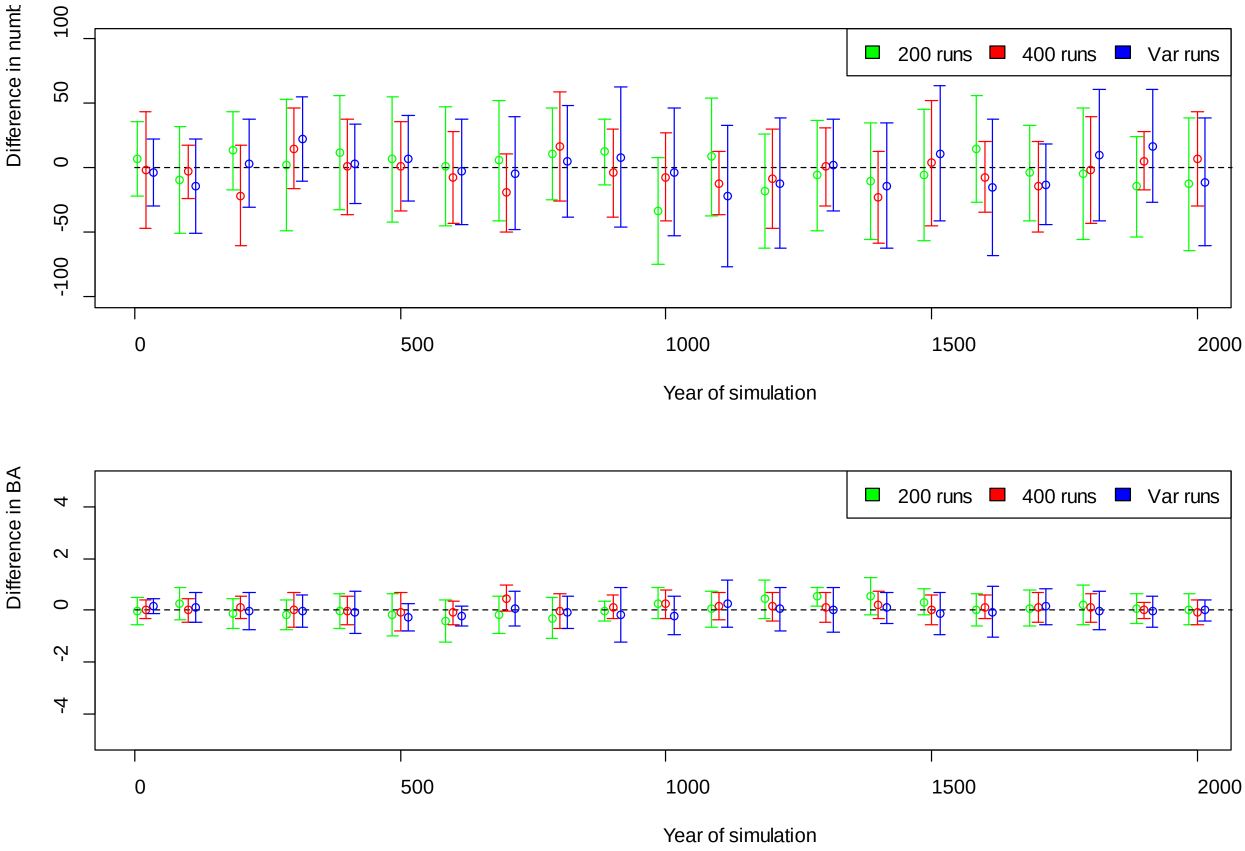


Fig. F1: Temporal changes in the predicted difference in N (*up*) and BA (b*ottom*) calculated with *nbruns* = 750 (reference) and *nbruns* = 200 (green), *nbruns* = 400 (red), and variable *nbruns* (blue). Mean and standard deviation of these differences were calculated based on each stratum.

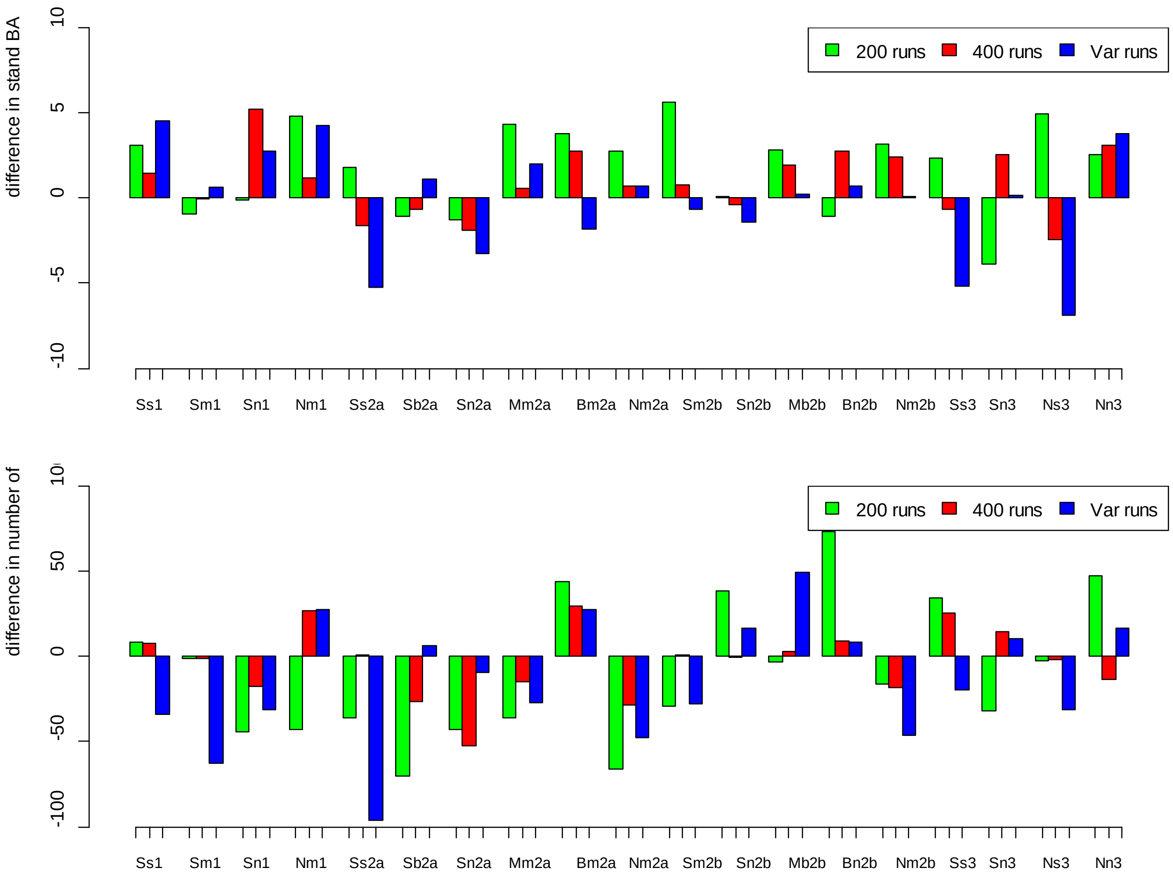


Fig. F2: Variability among strata in the predicted difference in N (*up*) and BA (b*ottom*) calculated with *nbruns* = 750 (reference) and *nbruns* = 200 (green), *nbruns* = 400 (red), and variable *nbruns* (blue) at simulation time = 100 years.

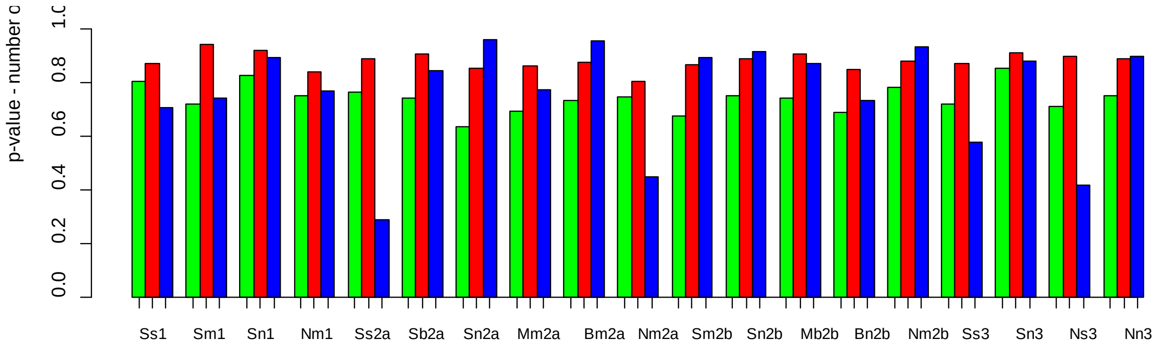


Fig. F3: Mean statistical difference (p-value of chi-square test) in species proportion in terms of N calculated over the 2000 years of simulation.

Appendix G: Effect of fluctuating browsing intensity on the PNV simulated for each stratum under current climate

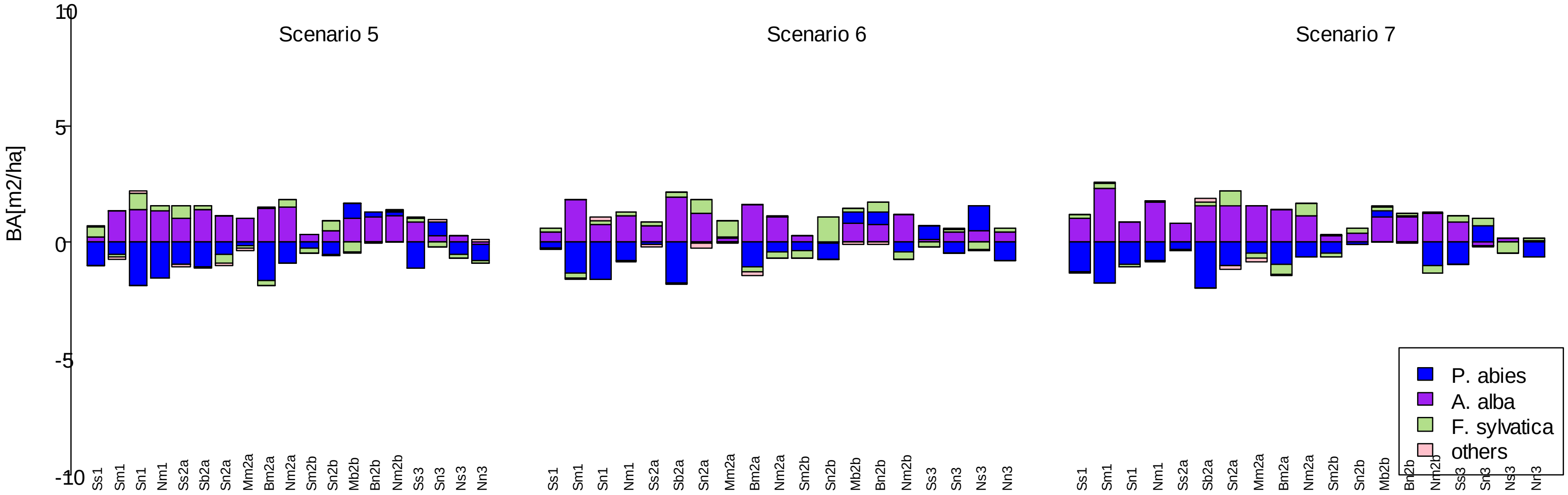


Fig. G1: Changes in species composition at pseudo-equilibrium due to fluctuating browsing intensity simulated for the 19 strata under current climate. For each scenario of fluctuating intensity with different wavelengths (respectively 20, 50 and 100 years for the scenarios 5, 6 and 7) the difference in BA was calculated compared with a constant average density (scenario 1) for *P. abies*, *A. alba*, *F. sylvatica* and the other species. Browsing aggregating parameter = 25m^2.

Table G1: Changes in species composition at pseudo-equilibrium due to fluctuating ungulates density averaged for the whole BFNP.

	Scenario 5		Scenario 6		Scenario 7	
Species	BA (m^2/ha [%])	Trs (nb/ha [%])	BA (m^2/ha [%])	Trs (nb/ha [%])	BA (m^2/ha [%])	Trs (nb/ha [%])
A. alba	+0.89 [+17.8]	+22.7 [+19.5]	+0.84 [+16.7]	+27.1 [+23.3]	+0.97 [+19.4]	+30.0 [+25.8]
P. abies	-0.58 [-2.5]	-19.9 [-3.6]	-0.52 [-2.2]	-15.6 [-2.8]	-0.65 [-2.8]	-1.2 [-1.3]
F. sylvatica	+0.00 [+0.1]	+4.2 [+4.3]	+0.18 [+3.4]	+3.9 [+4.1]	+0.08 [+1.4]	-4.3 [+4.4]
others	-0.01 [-0.8]	+28.8 [+13.5]	-0.03 [-4.6]	+26.3 [+12.4]	-0.02 [-3.1]	+34.1 [+16.0]

References

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Anlage 8:

Liste der Vorträge und Führungen über das Projekt 09/2009 bis 02/2014

Lfd. Nr.	Datum		Thema	Teilnehmer/Institution	Land	Anzahl Teilnehmer	Name
1	25.11.2009	Vortrag	Rothirschforschung	AG Rothirschmanagement der Regierung von Niederbayern	D	20	Dr. Heurich
2	14.4.2010	Vortrag	Wildtierforschung	Leibnitz Institut für Zoo- und Wildtierforschung Berlin	D	40	Dr. Heurich
3	21.03.2011	Vortrag	Individual based Movement Models	Workshop zu Spatio-temporal data in R	D		C. Dubke
4	30.08-3.09.2010	Vortrag	Home range dynamics of red deer (Cervus elaphus) at multiple scales	Tagung der Gesellschaft für Ökologie			M. Bevanda
5	15.04.2010	Vortrag	Towards a better understanding of animal movement patterns	BayCEER Workshop	D		M. Bevanda
6	23.3.2010	Vortrag	Rothirschforschung	Hochwildhegegemeinschaft Bayerischer Wald	D	30	Dr. Heurich
7	3.03.2011	Vortrag	Wildtierforschung	BJV Bezirksversammlung Niederbayern	D	100	Dr. Heurich
8	23.3.2011	Vortrag	Wildtierforschung	Akademie für Naturschutz und Landschaftspflege	D	10	Dr. Heurich
9	26.3.2011	Vortrag	Rothirschmanagement	Landesjägertag BJV	D	50	Dr. Heurich
10	29.3.2011	Vortrag	Wildtiermanagement und Forschung	Europarktagung	D	100	Dr. Heurich

				Wildtiermanagement			
11	7.06.2011	Vortrag	Temporal Habitat Preferences	Tagung der European Roe Deer Group	I, F, N, S, CZ, SLO, D, GB	40	C. Dubke
12	10.6.2011	Führung	Nationalpark, Wildtierforschung und Management	Tagung der European Roe Deer Group	I, F, N, S, CZ, SLO, D, GB	40	Dr. Heurich
13	5.-9.09.2011	Vortrag	Zeitliche Dynamik der Habitatnutzung	Jahrestagung der Gesellschaft für Ökologie			C. Dubke
14	5.-9.09.2011	Vortrag	Assessing the influence of forest structure on roe deer habitat selection	Jahrestagung der Gesellschaft für Ökologie			M. Ewald
15	5.-9.09.2011	Vortrag	The importance of landscape configuration for home range sizes of red deer	Jahrestagung der Gesellschaft für Ökologie			M. Bevanda
16	9.12.2011	Vortrag	Walks in the woods. Some steps in movement ecology.	Universität Potsdam			Prof. Dr. Reineking
17	7.11.2011	Vortrag	Wildtierforschung im Nationalpark Bayerischer Wald	Schweizer Hochschule für angewandte Wissenschaften	CH	10	Dr. Heurich
18	27.1.2012	Vortrag	Wildtierforschung und Management	TU München	D	15	Dr. Heurich
19	4.07.2012	Vortrag	What has movement ecology contributed to biodiversity research?	Universität Potsdam	D		Prof. Dr. Reineking

20	24.02.2013	Vortrag	Wildtiermanagement	Naturschutzzentrum Ruhestein	D	60	Dr. Heurich
21	18.4.2013	Führung, Vortrag	Rehforschung	Hochschule Weihenstephan	D/Fin	20	Dr. Heurich
22	14.09.2013	Vortrag	Wildtierforschung/Management	Uni Marburg	D	29	Dr. Heurich
23	10.4.2013	Führung, Vortrag	Rehforschung	Hochschule Weihenstephan	D	20	Dr. Heurich
24	22.05.2013	Vortrag	Verbissdruck und Nationalparkmanagement	Luchstagung der Nationalparkverwaltung	D,CH,A	150	Dr. Heurich
25	22.05.2013	Vortrag	Zeitliche Dynamik der Habitatnutzung,	Luchstagung der Nationalparkverwaltung	D,CH,A	150	C. Dubke
26	1.-5.09.2013	Vortag	Climate change and wildlife management interacting effects on forest dynamics in a protected area	TreeClim			M. Cailleret
27	9.-13.09.2013	Vortrag	Likely impacts of climate change on forest structure in the Bavarian Forest National Park	Jahrestagung der Gesellschaft für Ökologie			M. Cailleret
28	11.-15.8.2013	Workshop	Species distribution modelling und step selection functions	Universität Konstanz 'Summer school Animove'			Prof. Dr. Reineking
29	6.10.2013	Vortrag	Der Rothirsch im Nationalpark	Hirschtage der Nationalparkverwaltung	D	20	Dr. Heurich
30	4.12.2013	Vortrag	Flexible discrete choice models	Universität Freiburg	D	15	C. Dubke

Anlage 9:

GESCHÄFTSBEREICH LEBENSMINISTERIUM.BAYERN.DE

Nationalparkverwaltung
Bayerischer Wald

FACHTAGUNG

Erforschung der Ökologie von Luchs und Reh

22. und 23. Mai 2013
Waldgeschichtliches Museum St. Oswald

Nationalpark
Bayerischer Wald

Grußwort

In den 1980er-Jahren wurden insgesamt 17 Luchse auf tschechischer Seite ausgewildert. Diese Individuen bildeten im Wesentlichen den Grundstock für die heutige Luchspopulation im bayerisch-böhmischen Grenzgebiet. Der Luchs, unsere größte heimische Wildkatze fasziniert und polarisiert uns Menschen gleichzeitig. Viel wird in Jägerkreisen, in Naturschutzgruppen aber auch in der breiten Öffentlichkeit über ihn diskutiert und gesprochen. Für den Einen ist er ein faszinierender Teil der heimischen Tierwelt, für den Anderen ein unerwünschter Beutekonkurrent und für den Dritten schließlich ein Zeichen von Wildnis. Seine Rückkehr in die Wälder des ostbayerischen Grenzgebirges hat deutlich gezeigt, wie wenig wir letztendlich über seine Lebensweise, seine Arealansprüche oder über seine Populationsdynamik wissen.

Deshalb hat das Luchsprojekt des Nationalparks Bayerischer Wald in den letzten Jahren in Zusammenarbeit mit Jägern und Naturschützern Daten und Fakten über das Leben der Luchse und seiner Beutetiere in beiden Nationalparks und deren Vorfeld gesammelt. Mit konkreten wissenschaftlichen Erkenntnissen sollen Vorurteile abgebaut und die Akzeptanz verbessert werden. Mit der Fachtagung möchte die Nationalparkverwaltung Bayerischer Wald die Ergebnisse einer langjährigen Forschungsarbeit der Öffentlichkeit vorstellen und gemeinsam mit den verschiedenen Interessensgruppen diskutieren.

Hiermit sage ich allen, die an dem Gelingen des Projektes mitgewirkt haben herzlichen Dank und wünsche der Veranstaltung einen guten Verlauf.

Franz Leibl

Dr. Franz Leibl
Leiter der Nationalparkverwaltung

Anmeldeformalitäten

Die Veranstaltung ist kostenfrei. Eine Anmeldung ist jedoch notwendig, da die Teilnehmerzahl begrenzt ist.

Bitte senden Sie Ihre Anmeldung an die
Nationalparkverwaltung Grafenau, Raffaela Scala, Freyunger Straße 2, 94481 Grafenau,
raffaela.scala@npv-bw.bayern.de

Geben Sie bitte an, ob Sie ein Mittagessen am Mittwoch oder Donnerstag wünschen bzw. an der Grillfeier am Mittwoch Abend teilnehmen wollen.
Dafür wird jeweils vor Ort ein Unkostenbeitrag von 10 Euro erhoben.

Anmeldeschluss ist der 13.5.2013.

GESCHÄFTSBEREICH · LEBENSMINISTERIUM.BAYERN.DE

Nationalparkverwaltung
Bayerischer Wald

Mittwoch, 22. Mai 2013		
10.00 Uhr	**Begrüßung**	**Jörg Müller** Nationalparkverwaltung Bayerischer Wald **Wolfgang Schröder** Sprecher des Wissenschaftlichen Beirates
10:15 Uhr - 12:00 Uhr	**Wechselwirkungen zwischen Reh, Rothirsch und der Waldverjüngung**	
	Auswirkungen von Störungen auf die Nahrungsverfügbarkeit von Reh und Rothirsch	**Thorsten Zeppenfeld** Nationalparkverwaltung Bayerischer Wald
	Huftiermanagement in einem Nationalpark. Unbeabsichtigte Effekte auf die Verteilung des Verbissdrucks	**Marco Heurich** Nationalparkverwaltung Bayerischer Wald
	Der Einfluss von Huftieren auf die Überlebenswahrscheinlichkeit der Waldverjüngung	**Christian Clasen** Technische Universität München
	Likely effects of changes in climate and browsing intensity on the Bavarian Forest National Park: a modeling approach	**Cailleret Maxime** Eidgenössisch Technische Hochschule Zürich
11:45 Uhr – 12:45 Uhr	**Mittagspause**	
12:45 Uhr – 15:00 Uhr	**Was steuert die Raumnutzung von Luchs, Reh und Rothirsch im Böhmerwaldökosystem?**	
	Zur Stressbelastung des Rehwildes beim Fang mit der Kastenfalle	**Georg Weilnböck** Nationalparkverwaltung Bayerischer Wald
	Influence of tourism and traffic on the activity and space use of Lynx lynx	**Elisa Belotti** Nationalparkverwaltung Sumava
	Reh und Rothirsch auf der Spur: Einblicke in die zeitliche Dynamik der Habitatnutzung	**Claudia Dubke** Universität Bayreuth
	Wieviele Luchse haben Platz im Böhmerwald. Ein Habitatmodell für die Luchspopulation.	**Nora Magg** Nationalparkverwaltung Bayerischer Wald

Tagung zur Luchforschung

Vom 22. – 23. Mai 2013
Waldgeschichtliches Museum, St. Oswald

Vortragsprogramm

Nationalpark
Bayerischer Wald

	Auch nach 25 Jahren noch am Nationalparktropf – Luchse in Ostbayern	**Jörg Müller** Nationalparkverwaltung Bayerischer Wald
15:00 Uhr – 15:30 Uhr	**Kaffeepause**	
15:30 Uhr – 17:30 Uhr	**Der Luchs und seine Beutetiere**	
	Wie tickt die Uhr von Reh und Hirsch? Aktivitätsrhythmen bei den Beutetieren des Luchses	**Annette Krop-Benesch** Leibniz-Institut für Gewässerökologie und Binnenfischerei
	Zur Nahrungsökologie des Luchses.	**Kathrin Mayer** Nationalparkverwaltung Bayerischer Wald
	Wie viele Rehe frisst ein Luchs? Prädationsraten von Luchsen im Böhmerwald	**Nicole Weder** Universität Greifswald
	Hängt die Risswahrscheinlichkeit der Rehe von deren Verhalten ab	**Ulrike Märkel** Universität Tübingen
	Survival und Mortalitätsursachen von Rehen unter Luchsprädation	**Klara Zeis** Uni München
	Top-Down-Effekte im Luchs-Reh-System. Ein Modellansatz	**Robert Hagen** Universität Freiburg
Ab 19:00	**Grillfest auf der Bärnlochhütte**	

Donnerstag, 23. Mai 2013		
8:30 Uhr – 9:40 Uhr	**Monitoring von Luchsen und Huftieren**	
	Genetic monitoring of the Bohemian forest lynx population	**Kristina Danizowa** Nationalparkverwaltung Sumava
	Flugzeuggestütztes Monitoring von Großsäugern mit kombinierten thermal- und visuellen Kameras	**Ulrich Franke** Ingenieurbüro Aerosense
	Monitoring von Luchsen mit Fotofallen	**Kirsten Weingarth und Christoph Heibl** Nationalparkverwaltung Bayerischer Wald
9:45 Uhr – 11:45 Uhr	**Akzeptanz von Wildtieren**	
	Rothirsch auf neuen Irrwegen. Eine politikwissenschaftliche Analyse	**Jutta Gerner** Universität Freiburg
	Vergleichende Untersuchungen zur Akzeptanz des Luchses	**Ulrich Schraml** Universität Freiburg
10:45 Uhr – 11:15 Uhr	**Kaffeepause**	
11:00 Uhr – 12:00 Uhr	**Resümee und Diskussion**	
	The Lynx project. What have we learned ? Implications for management? The Czech perspective.	**Ludek Bufka** Nationalparkverwaltung Sumava
	Das Luchsprojekt. Was haben wir gelernt und wie können wir das Luchsmanagement weiterbringen?	**Marco Heurich** Nationalparkverwaltung Bayerischer Wald
	„Netzwerk und Teamwork: ein produktiver Forschungsansatz“	**Wolfgang Schröder** Sprecher des Wissenschaftlichen Beirates
12:00 Uhr – 13:00 Uhr	**Mittagspause**	
13:00 Uhr – 16:00 Uhr	**Beratungen des Wissenschaftlichen Beirates (nicht öffentlich)**	

Finanzierung

ZIEL 3
CÍL 3

WWF

DBU

Bayerisches Staatsministerium für
Ernährung, Landwirtschaft und Forsten

Tagung zur Luchsforschung

Vom 22. – 23. Mai 2013
Waldgeschichtliches Museum, St. Oswald

Vortragsprogramm

Nationalpark
Bayerischer Wald