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Habitatmodelle und Konnektivitätsanalysen bei tagaktiven Schmetterlingen

(Habitat models and connectivity analysis for butterflies and moths)

Birgit Binzenhöfer

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Birgit Binzenhöfer
aus Limbach/Main

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Department Naturschutzforschung &
Department Biozönoseforschung
UFZ – Umweltforschungszentrum
Leipzig-Halle
Permoserstr. 15
04318 Leipzig

Fachbereich Biologie
Martin-Luther-Universität
Halle-Wittenberg
Weinbergweg 10
06099 Halle/Saale

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Chapter I

Einführung

ALLGEMEINE EINLEITUNG UND ZIELSETZUNG

Insbesondere in den letzten Jahrzehnten sind landwirtschaftliche Intensivierung (Petit et al. 2003) und Nutzungsaufgabe (BFN 2003, Sutcliffe et al. 2003) die Hauptursachen für den Biodiversitätsverlust in Westeuropa. Besonders betroffen von dieser Entwicklung sind extensiv genutzte Wiesengesellschaften, wie Halbtrocken- und Trockenrasen (Blab & Kudrna 1982, Plachter 1991). Unter allen Tier- und Pflanzengruppen wiederum sind die Artenverluste bei Insekten in Kulturlandschaften besonders hoch (Thomas 1984, 1991, Thomas & Morris 1994). Ein gravierender Artenrückgang ist insbesondere unter den Tagfaltern und Widderchen zu verzeichnen (vgl. Bourne & Thomas 2002).

Zum Erhalt der biologischen Vielfalt sind genaue Kenntnisse über die spezifischen Habitatansprüche der einzelnen Arten sowie insbesondere in Kulturlandschaften über die Auswirkungen verschiedener Landnutzungsmaßnahmen erforderlich. Die Analyse von Art-Umwelt-Beziehungen spielt deshalb eine zentrale Rolle in der Ökologie (Guisan & Zimmermann 2000).

Statistische Habitatmodelle auf der Basis von Präsenz-Absenz-Daten der Arten, in Beziehung gesetzt zu den entsprechenden Umweltbedingungen, stellen eine geeignete Methode dar, die Habitateignung einer Fläche zu quantifizieren (Morrison et al. 1998, Kleyer et al. 1999, Schröder 2000) und Schlüsselfaktoren für das Vorkommen herauszuarbeiten (Kleyer 1999). Daneben können sie auch als wertvolles Instrument zur Vorkommensprognose in anderen Gebieten (z.B. Cowley et al. 2001, Schadt et al. 2002) oder zur Einschätzung der Überlebensfähigkeit einer Art dienen (Biedermann & Schröder 2002). Habitatmodelle besitzen dadurch ein großes Anwendungspotential in der Naturschutzforschung und –praxis (Scott et al. 2002, Reineking & Schröder 2003).

Das Vorkommen einer Art hängt neben der Habitatqualität auch von der Größe und räumlichen Anordnung der geeigneten Habitate ab (Hanski & Gilpin 1997, Thomas et al. 1992, 2001, Wahlberg et al. 2002). Gemäß der Metapopulationstheorie können geeignete Habitate auch unbesetzt sein, wenn sie beispielsweise zu klein oder zu isoliert sind (Hanski & Gilpin 1997). Kleinere Populationen sterben in der Regel schneller aus (Wilcox 1980, Hovestadt 1990, Poethke et al. 1996, Settele 1998, Veith & Klein 1996) und die Wahrscheinlichkeit der Wiederbesiedlung erloschener (Teil-)Populationen wird aufgrund der eingeschränkten Habitatvernetzung reduziert (Hanski 1994b). Neben Habitatverlust führt Landschaftsfragmentierung zum Rückgang vieler Arten (Kaule 1986, Caughley 1994, Fahrig & Merriam 1994, Settele et al. 1996).
Inwieweit die Verinselung bzw. Vernetzung von Lebensräumen die Organismenverteilung in einer Landschaft bestimmt, wird im Rahmen von Konnektivitätsanalysen untersucht. Dabei werden Größe und räumliche Anordnung der Landschaftselemente in Bezug zur Habitatbesetzung gesetzt. Auf diese Weise kann neben der Habitatqualität auch der Einfluss der Landschaftsstruktur auf das Vorkommen einer Art bei der Habitatmodellbildung berücksichtigt werden.

Die vorliegende Arbeit ist in das Forschungsverbundprojekt MOSAIK (Kleyer et al. 2002) eingebettet, das den Einfluss unterschiedlicher Managementverfahren auf die Überlebenswahrscheinlichkeit von Fauna und Flora in trockenen, überwiegend nährstoffarmen Grünlandbiotopen untersucht. Sie beschäftigt sich in erster Linie mit der Fragestellung, welche Habitatparameter das Vorkommen verschiedener Lepidopterenarten bestimmen. Dazu wurden Habitatmodelle für die tagaktiven Falterimagines von *Zygaena carniolica* (LINNAEUS 1761; Zygaenidae), dem Esparsetten-Widderchen, und *Coenonympha arcania* (SCOPOLI 1763; Nymphalidae), dem Weißbindigen Wiesenvögelchen, entwickelt. Darauf aufbauend wurde die Prognosefähigkeit dieser Modelle getestet und Habitateignungskarten für das gesamte Hauptuntersuchungsgebiet, das Naturschutzgebiet „Hohe Wann“ in den Hassbergen (Bayern), erstellt (Kap. II). Neben der zeitlichen und räumlichen Validierung (Vergleichsuntersuchungsgebiet NSG „Leutratal“ bei Jena, Thüringen) der Habitatmodelle (Kap. II, IV) wurde ihre Übertragbarkeit auch auf die jeweils anderen untersuchten Arten bzw. auf andere Insektengruppen (Laub- und Feldheuschrecken) untersucht (Kap. III). Auf der Basis der Präimaginalstadien wurden des weiteren Habitatmodelle von *Cupido minimus* (FUESSLI 1775; Lycaenidae), dem Zwergbläuling, entwickelt. Zusätzlich konnte der Effekt der räumlichen Konfiguration der

Wirtspflanzenbestände auf die Extinktions- und Kolonisationsraten dieser Art analysiert werden (Kap. IV). Für alle drei Falterarten wurde der Einfluss der Habitatqualität und Konnektivität auf die Habitatbesetzung untersucht (Kap. II, IV).

Die Ergebnisse aus den Habitatmodellen und der Habitatkonnektivitätsanalyse bilden die Basis für Szenarien (mittels Computersimulation), die den Einfluss verschiedener Bewirtschaftungsmethoden auf die langfristige Überlebenswahrscheinlichkeit von Falterpopulationen beurteilen (Schröder et al. 2004). Damit liefert die vorliegende Arbeit einen wichtigen Baustein zur Einschätzung des Aussterberisikos von Arten unter verschiedenen Umweltbedingungen.

KONZEPTIONELLER HINTERGRUND

Habitat und Habitatmodellierung

Als ein Habitat bezeichnet man den Teil der Umwelt, in welcher eine bestimmte Art überleben und sich reproduzieren kann (Odum 1971), samt der in diesem Raum vorkommenden biotischen und abiotischen Elemente (Morrison & Hall 2002). Das Nischen-Konzept ist in diesem Sinne restriktiver: es beschränkt sich auf jene Faktoren, die für die jeweilige Art (überlebens-)relevant sind. Da die Anwesenheit von Parasiten, Räubern und Konkurrenten die Persistenz einer Art beeinflussen kann, unterscheidet man zwischen fundamentaler ökologischer und realisierter ökologischer Nische (Malanson et al. 1992, Morrison & Hall 2002). Während die fundamentale ökologische Nische einen n-dimensionalen Raum beschreibt, in welchem eine Art potentiell lebensfähige Populationen erhalten kann, umfasst die realisierte ökologische Nische den Teilraum, der aufgrund von Interaktionen mit der Umwelt auch tatsächlich besetzt wird (Morrison & Hall 2002). Aufgrund ihres empirischen Charakters beschreiben statistische Habitatmodelle die realisierte Nische (Austin et al. 1990, Guisan & Zimmermann 2000).

Die Habitatmodellierung verfolgt zum einen das Ziel, das Verständnis von Art-Habitat-Interaktionen zu verbessern und Habitatansprüche von Arten zu quantifizieren (Morrison et al. 1998, Peeters & Gardeniers 1998, Kleyer et al. 1999). Zum anderen liefert sie Prognosen für das räumliche Verteilungsmuster von Arten (Cowley 2000 et al., Schröder & Reinecking 2004a, Scott et al. 2002). Die Kombination aus beiden Aspekten ermöglicht eine differenzierte Bewertung der Habitateignung von Flächen hinsichtlich der untersuchten Arten in einer konkreten Landschaft (z.B. Brooks 1997, Lutze et al. 1998, Ritters et al. 1997) und liefert Informationen zu den Auswirkungen von Eingriffen oder Ausgleichs- und Pflegemaßnahmen im Naturschutzmanagement (Kleyer et al.1999, Schröder 2000).

Habitatmodelle besitzen statischen Charakter (Guisan & Zimmermann 2000), da aufgrund der vergleichsweise geringen Lebenserwartung der Organismen eine Quasi-Gleichgewichtssituation zwischen dem Vorkommen einer Art und den Umweltbedingungen angenommen wird (Austin 2002, Kleyer et al. 1999, Guisan & Zimmermann 2000, Guisan et al. 2002). Dennoch kann die Dynamik einer Landschaft bzw. eines Habitates – beispielsweise als Frequenz von Störungsereignissen innerhalb eines Managementregimes – in Form einer Habitateigenschaft in das Modell integriert werden (Schröder et al. 2004). In Verbindung mit Populationsgrößenschätzungen können Habitatmodelle auch kritische Populationsgrößen für das Überleben von Arten schätzen (Biedermann 1997). Stehen zusätzliche Informationen zu Dispersion, Natalität und Mortalität zur Verfügung, kann die Populationsdynamik im Rahmen einer Populationsgefährdungsanalyse (Gilpin & Soule 1986, Hovestadt et al. 1991, Settele et al. 1996) oder in räumlichen (Meta-)Populationsmodellen simuliert werden (Grimm et al. 1994, Söndgerath & Schröder 2002, Wahlberg et al. 1996).

Im Gegensatz zu literaturbasierten Habitatmodellen, die aus verbal formulierten Beobachtungen und Literaturangaben erstellt werden, basieren statistische Habitatmodelle auf Auswertungen empirischer Untersuchungen. Dadurch enthalten sie konkrete quantitative Aussagen darüber, wie zuverlässig die gefundenen Beziehungen die zugrunde liegenden Hypothesen zum Vorkommen der Art erklären (Kuhn & Kleyer 1999a). Zudem zeichnen sich statistische Habitatmodelle durch eine größere Objektivität aus (Kuhn 1998), was ihre Akzeptanz bei Planungsentscheidungen in der Naturschutzpraxis fördern sollte (Morrison et al. 1998).

Bedingt durch hohe Populationsdynamik und Saisionalität kann die Aktivitätsdichte von Arten starken Schwankungen unterliegen (den Boer 1990), so dass zur Modellbildung die Verwendung von binären Päsenz-Absenz-Daten verlässlicher scheint als die von Abundanzdaten, zumal Habitatmodelle auch zur Vorkommensprognose von Arten dienen (van Horne 1983). Ein geeignetes Verfahren zur Habitatmodellierung auf der Basis von Päsenz-Absenz-Daten ist die logistische Regression (Hosmer & Lemeshow 2000, Jongman et al. 1995, Trexler & Trevis 1993). Hierbei wird geprüft, ob der Zusammenhang zwischen der Inzidenz einer Art (Response-Variable) und der Ausprägung einer oder mehrerer Umweltvariablen (Prädiktor-Variablen) signifikant durch ein logistisches Modell beschrieben werden kann (Fielding & Haworth 1995). Dabei ist die geschätzte abhängige Variable auch als

Vorkommenswahrscheinlichkeit oder Habitateignung interpretierbar und nichtlinear von den Habitatfaktoren abhängig (Kleyer et al. 1999). Die logistische Regressionsgleichung lautet:

$$P(y=1)=\frac{e^{\beta_0+\beta_1 x_1+\ldots+\beta_k x_k}}{1+e^{\beta_0+\beta_1 x_1+\ldots+\beta_k x_k}}=\frac{1}{1+e^{-(\beta_0+\beta_1 x_1+\ldots+\beta_k x_k)}} \quad (1)$$

$P(y=1)$	Wahrscheinlichkeit, dass die abhängige Variable 1 ist (d.h. die Art vorkommt)
$ß_0$	Konstante
x_k	unabhängige Variable
$ß_k$	Koeffizient der unabhängigen Variablen

Um den Gültigkeitsbereich von Habitatmodellen zu überprüfen, muss ihre Übertragbarkeit getestet werden. Sonst besteht die Gefahr, dass die Modelle zu sehr an den zugrunde liegenden Datensatz angepasst sind und zu optimistische Werte bezüglich der Modellgüte liefern (Fielding & Haworth 1995, Verbyla & Litvaitis 1989, Schröder & Reineking 2004b). Dies ist umso mehr von Bedeutung, wenn die Modellergebnisse als Grundlage für Handlungsentscheidungen in der Naturschutzpraxis dienen (Lutze et al. 1998, Schröder 2000). Im Rahmen der Validierung von Habitatmodellen erfolgt die Modellbewertung auf der Grundlage von Stichproben, die nicht zur Modellschätzung herangezogen wurden (Schröder & Reinecking 2004b). Am besten werden dabei unabhängige, externe Daten verwendet, die in anderen Untersuchungsjahren und –räumen aufgenommen wurden. Somit kann kritisch überprüft werden, ob die Bedingungen bei der Modellerstellung (naturräumliche und klimatische Verhältnisse, populationsökologische Dynamik) auch auf andere zu bewertende Systeme (andere Gebiete oder andere Jahre) übertragen werden können (Kuhn & Kleyer 1999b). Stehen keine externen Daten zur Verfügung, so kann die Validierung zumindest intern über sogenannte Resampling-Verfahren erfolgen. Dabei wird ein Teil eines Datensatzes (Trainingsdatensatz) zur Modellkalibrierung (Anpassung) und der andere Teil (Testdatensatz) zur Abschätzung der Modellgüte verwendet (Guisan & Zimmermann 2000, Schröder 2000). Bewährte Resampling-Methoden sind beispielsweise das Bootstrap-Verfahren oder die Kreuzvalidierung (Schröder & Reineking 2004b). Im Bootstrap-Verfahren wird durch zufälliges Ziehen eine Stichprobe aus dem Gesamtdatensatz (mit Zurücklegen) erzeugt. Dieser Bootstrap-Datensatz wird dann als Trainingsdatensatz zur Modellbildung verwendet, während die Orginaldaten als Testdatensatz zur Evaluierung dienen. Aus der Differenz der Vorhersagegüte von Trainings- und Testdatensatz wird der sog. „Optimismus" des Modells geschätzt. Zur Ermittlung der validierten Modellgüte wird dann (nach meist mehr als 100-maliger Widerholung) der durchschnittliche Optimismus von den ursprünglichen Gütewerten subtrahiert (Efron & Tibshirani 1993, Reineking & Schröder 2003, Schröder & Reineking 2004b). Bei der zehnfachen Kreuzvalidierung, wie sie hier angewendet wurde, wird der Gesamtdatensatz zufällig in zehn gleich große Teile aufgeteilt. Auf der Grundlage der ersten neun Zehntel (Trainingsdatensatz) werden dann die Modellkoeffizienten geschätzt und das restliche Zehntel (Testdatensatz) dient zur Bestimmung der Modellgüte. Dieser Vorgang wird zehnmal wiederholt, wobei jedesmal Test- und Trainingsdatensatz vertauscht werden, so dass jeweils eine andere Stichprobengruppe als Testdatensatz zur Modellvorhersage dient. Schließlich werden die Mittelwerte der Gütekriterien der Testdatensätze zur Einschätzung der tatsächlichen Modellgüte herangezogen (Reineking & Schröder 2003).

Metapopulation und Habitatkonnektivität nach Hanski (1994b)

Viele früher zusammenhängende Lebensräume sind durch menschliche Aktivitäten in den letzten Jahrzehnten fragmentiert worden. Für verschiedene Lebensgemeinschaften führt diese Inselbildung zum Aussterben von Populationen (Blaschke 1999). Die Etablierung eines geeigneten Habitatnetzwerkes spielt deshalb eine zentrale Rolle in der Naturschutzbiologie (Baguette 2000). Wenn ein ausreichendes, räumliches Netzwerk von kleinen Habitaten den Individuenaustausch zwischen lokalen Populationen von Arten ermöglicht, kann die regionale Population in einer Landschaft stabilisiert werden (Kuhn & Kleyer 1999b). Prozesse, welche das Überleben von Arten in einem Habitatnetzwerk erlauben, werden im sog. Metapopulationskonzept integriert (Hanski & Gilpin 1991; 1997). Die Metapopulationstheorie beruht auf der Annahme, dass eine Art trotz lokalen Aussterbens regional überleben kann, wenn Wiederbesiedlung von benachbarten diskreten Lebensräumen erfolgt (Settele 1998). Nach Reich & Grimm (1996) ist eine Metapopulation „eine (regionale) Population von (lokalen) Populationen“, die im „klassischen“ Sinne (Hanski & Gilpin 1997) drei Bedingungen erfüllt:

1. Die lokalen Populationen besitzen eine asynchrone Dynamik und sind von anderen lokalen Populationen abgrenzbar.
2. Alle Patches (Habitate) bzw. Lokalpopulationen sind potentiell vom Aussterben bedroht.
3. Zwischen den einzelnen Habitaten besteht ein Individuenaustausch, so dass (Neu-) Kolonisation erfolgen kann.

Auch wenn nicht immer eine Metapopulation im „eigentlichen" Sinne vorliegt, lassen sich doch viele Grundphänomene der räumlichen Beziehungen von Populationen zueinander über metapopulationsartige Grundmuster besser verstehen und erklären (Settele 1998).

In der Metapopulationsbiologie wird der Einfluss der räumlichen Anordnung von geeigneten Habitaten auf das Überleben einer Metapopulation untersucht. Dabei ist es nicht ausreichend, das Artvorkommen zur Distanz zu potentiell benachbarten Habitaten zu korrelieren. Vielmehr kann der Isolationseffekt nur dann festgestellt werden, wenn bei der Analyse Informationen über die Habitatbesetzung der benachbarten Patches ebenfalls einfließen. Das Konnektivitätsmaß S nach Hanski (1994b) berücksichtigt neben Anzahl, Größe und Entfernung auch die Besiedlung der betrachteten Art in benachbarten Habitaten, um das Vorkommen von Tierpopulationen in fragmentierten Landschaften zu erklären. Mit diesem Parameter ist es möglich, den artspezifischen Effekt der Isolation zur Beurteilung der Überlebensfähigkeit von Organismen in die Habitatmodellbildung zu integrieren (Kuhn & Kleyer 1999b).

In Kapitel IV dieser Arbeit wurde neben der Habitatqualität auch der Einfluss von Flächengröße und Konnektivität nach Hanski (1994b) in den Habitatmodellen von *C. minimus* untersucht. Zudem wurde die Abhängigkeit der Extinktions- und Kolonisationsereignisse dieser Art von der räumlichen Verteilung der Raupennahrungspflanze (*Anthyllis vulneraria*) analysiert. Als Grundlage dazu diente eine vollständige Erfassung der Präimaginalstadien in allen potentiellen Lebensräumen (Flächen mit Raupenfutterpflanze) des Hauptuntersuchungsgebietes in den Jahren 2001 und 2002.

Habitatkonnektivitätsanalyse nach einem Ansatz von Keitt et al. (1997)

Da der Nachweis von *Z. carniolica* und *C. arcania* über die Präimaginalstadien wenig effektiv (vgl. auch Hermann 2000) und sehr aufwändig ist, wurden im Rahmen dieser Untersuchung die Falterimagines auf ausgewählten Zufallsprobeflächen erhoben. Eine Auswertung der Konnektivität nach Hanski (1994b) war aufgrund der fehlenden flächendeckenden Lebensraumkartierung nicht möglich. Die Habitatkonnektivitätsanalyse erfolgte für diese beiden Arten nach einem Ansatz von Keitt et al. (1997, cf. Schröder 2000) (Kap. II). Im Vergleich zur Hanski-Methode hat dieses Verfahren jedoch den Vorteil, dass zur Quantifizierung der Habitatvernetzung neben der Größe auch die Dichte und Form der Patches berücksichtigt werden, welche das Dispersal und damit die Austauschprozesse zwischen den einzelnen Habitaten beeinflußen (Gustafson & Gardner 1996, Moilanen & Hanski 1998, Taylor et al. 1983).

Die Habitatkonnektivitätsanalyse nach Keitt et al. (1997) beruht auf der Perkolationstheorie (Stauffer & Aharony 1991) und Theorie der Landschaftsgraphen (Cantwell & Forman 1993). In Anlehnung an Schröder (2000) werden alle Habitat-Patches eines Untersuchungsgebietes, für die das Vorkommen einer Art durch die Habitatmodelle prognostiziert worden ist, als Polygonflächen in einem Geographischen Informationssystem (ArcView) dargestellt. Auf der Basis dieser dichotomisierten Habitateignungskarte werden anschließend diejenigen Habitat-Patches zu Habitat-Clustern zusammengefasst, deren Außengrenzen nicht weiter als die maximale Ausbreitungsdistanz der Art entfernt liegen. Die Korrelationslänge (correlation length) dient als Index zur Berechnung der Habitatkonnektivität. Sie entspricht der durchschnittlichen Distanz, die sich ein Individuum, das zufällig in einem Habitat-Cluster plaziert wurde, bewegen kann, bis es eine Cluster-Grenze erreicht (Keitt et al. 1997). Die Korrelationslänge stellt damit einen aussagekräftigen Landschaftsindex dar (Gardner et al. 1993).

Chapter II

Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*

Birgit Binzenhöfer, Boris Schröder, Robert Biedermann,
Barbara Strauß and Josef Settele

IN PREP. FOR BIOLOGICAL CONSERVATION

Abstract

We developed habitat models basing upon logistic regression analysis for adult populations of the burnet moth Zygaena carniolica and the nymphalid butterfly Coenonympha arcania in Northern Bavaria, Germany. The relation between adult occurrence and habitat parameters (including the influence of the landscape context) has been analyzed on 139 sites.

Presence of the burnet is mainly explained by the presence of nutrient-poor dry grasslands and the presence of nectar plants in the direct vicinity (mainly within a radius of 25 m), that of the nymphalid by larger areas of extensively used dry grasslands in a surrounding of 200 m in combination with small patches of higher shrubs and bushes. The optimal date of management for C. arcania is after the 15th of July or non- resp. irregularly usage. The models yielded satisfactory precision in spatially explicitly predicting the occurrence of both species by only including the parameter "biotope type" into the models. Thus, the creation of habitat suitability maps for the whole area of investigation was possible for both species.

Internal as well as external validation indicated the robustness and general applicability of the models. Their transferability in time and space indicates their high potential relevance for applications in nature conservation.

Because of the high amount of suitable habitat in the study area, habitat connectivity analysis have not shown any effects of isolation, habitat size or configuration in both species.

INTRODUCTION

Agricultural intensification on the one hand and abandonment of traditional, economically unsustainable land use practices on the other hand are the main reasons for the loss of biodiversity in large parts of Europe (Petit et al. 2003, BFN 2003, Sutcliffe et al. 2003). In order to stop the decline of species, monitoring can provide a profound basis for the assessment of effects of land use changes (Niemelä 2000). Habitat models, which formalize the relation between the occurrence of a species and the characteristics of a site (Kleyer 1999), may be a cost efficient alternative to monitoring (Owen 1989, Fraser 1998). This is especially the case if their robustness and validity is shown so that they can be applied to predict the spatial distribution in less well studied regions (Verbyla & Litvaitis 1989, Schröder & Richter 1999, Pearce & Ferrier 2000a, Cowley et al. 2001). Through the qualitative and quantitative key factor analysis (Austin et al. 1990, 1996, Pearce et al. 1994, Kleyer et al. 1999) they are also suited to assess the survival probability of species (Kleyer 1999, Biedermann & Schröder 2001).

In this context we developed habitat models for a burnet moth (*Zygaena carniolica* LINNAEUS 1761) and a nymphalid butterfly (*Coenonympha arcania* SCOPOLI 1763). We hypothesize (1) that the presence of the adults can be predicted by a limited set of habitat parameters, including features regarding the surrounding landscape, and (2) that the models can be applied in other regions.

The present management regimes of industrialized countries strongly promote habitat fragmentation, i.e. reduce habitat connectivity, which are assumed to be important features for species occurrence and population survival in fragmented landscapes (Fahrig & Merriam 1985, Hanski 1994a, van Langevelde 2000, Ferreras 2001, Eon et al. 2002). According to Taylor et al. (1993), connectivity is the degree to which the landscape facilitates or impedes exchange of individuals with other resource patches. Therefore we test, how patch occupancy is affected by habitat connectivity.

MATERIALS AND METHODS

Research areas

The main study area is the nature reserve "Hohe Wann" in Northern Bavaria (50° 03' N, 10° 35' E). Elevations range from 240 to 390 m asl. and the geographical formation of the region is Middle Keuper. Average annual temperature is 8.8 °C, average annual precipitation 650 mm (Deutscher Wetterdienst 2002). While agriculture still prevails in leveled areas (i.e. valleys and plateau sites), the hilly parts are only extensively used or abandoned. They form a small-scale mosaic of dry grasslands with mesoxerophytic meadows, thermophilous fringes, scattered bushes and (largely abandoned) vine yards (Schröder et al. 2004).

The study area for spatial validation is located 200 km north near the city of Jena (Thuringia). This study sites include a part of the nature reserve "Leutratal" and adjacent areas and are stamped by the shell limestone layers of the river Saale valley. Elevations range from 190 to 260 m asl., average annual temperature is 9.3 °C and average annual precipitation is 587 mm (Heinrich et al. 1998). It is characterized by extensively used mesophilous grasslands in combination with mesoxerophytic meadows and thermophilous fringes. The more or less south-facing slopes are characterized by numerous hedgerows and bushes (Heinrich et al. 1998, pers. observ.).

Study species

Zygaena carniolica is a xerothermophilous species of fallow, moderately grazed or mown dry grasslands. It is listed as endangered for Bavaria as well as entire Germany (Bayerisches Landesamt für Umweltschutz 2003, Pretscher 1998). Within the research areas the larvae feed on *Onobrychis viciifolia* and *Lotus corniculatus*. Adults prefer violet flowering nectar plants like *Knautia arvensis*, *Scabiosa columbaria*, and *Centaurea* species. Visits also have been observed on *Origanum vulgare* and *Onobrychis viciifolia* (detailed information on biology in Ebert & Rennwald 1994, Weidemann & Köhler 1996, SBN 1997, Kreusel & Böhmer 1998).

Coenonympha arcania inhabits dry grasslands with abundant bushes as well as mesophilous grasslands near hedges and forest edges. The species is regarded as near threatened in Bavaria and in Germany (Bayerisches Landesamt für Umweltschutz 2003, Pretscher 1998). Larvae preferably feed on nutrient poor grasses like *Holcus lanatus*, *Brachypodium pinnatum*, *Festuca ovina* or *Melica* species. Requirements for nectar plants are unspecific, but also incompletely assessed (for biology see: Weidemann 1995, Ebert & Rennwald 1991, SBN 1991, Settele et al. 2000).

Methodology

Selection and characterization of study sites, sample plots, predictor variables, and incidence recording of adults

We selected 139 plots within the main study area in 2001 in a randomly stratified way (Guisan & Zimmermann 2000, Hirzel & Guisan 2002). Based on a detailed map, ten relevant biotope types have been defined as strata by means of GIS-analysis (ESRI ArcView). In each of these strata the upper left corners of 30 x 30 m^2-plots have been randomly selected. The strata in which the probability of either presence or absence of the respective species was expected to be high (according to published information) have been sampled less intensively than the ones, where one could expect further habitat parameters to have an impact on the incidence (Table 1). For the purpose of spatial validation, three plots have been selected in each of six different strata in a second study area. The strata missing there also have been of minor importance in the main study area. Therefore the number of plots also has been reduced from 2001 to 2002 in the main study area.

Table 1: Sample plots, their distribution across types of biotope and the frequency of occurrence of *Z. carniolica* and *C. arcania*.

biotope type	**plots**	**species**	**plots**	**species**	**plots**	**species**
	H. Wann 2001	**presence *Z. carn./C. arc.***	**H. Wann 2002**	**presence *Z. carn./C. arc.***	**Leutra 2002**	**presence *Z. carn./C. arc.***
arable land	7	- /-	-	- /-	-	- /-
fallow land	7	- / 1	7	1 / 1	-	
intensively managed meadow	8	- / 2	8	- / 2	3	
inten. managed meadow, meagre	19	- / 3	19	1 / 4	3	- / 2
extensively managed meadow	43	13 / 23	43	14 / 20	3	1 / 2
mesoxerophytic grassland	24	16 / 13	24	12 / 15	3	2 / 3
fringe vegetation, thermophile	11	5 / 11	11	4 / 11	3	2 / 3
hedge & bushes	6	- / 6	6	- / 5	3	1 / 3
thermophilic oak forest	7	- / -	-	- / -	-	- / -
forest without thermoph. oak forest	7	- / -	-	- / -	-	- / -

In each plot we quantified habitat parameters (Table 2), including neighboring strata, as incidence might also be influenced by the surrounding landscape structure and heterogeneity (Fahrig & Johnson 1998). Based on the map of biotopes, which covers the entire research area, parameters of the surroundings have been quantified via GIS applications; e.g. proportion of mesoxerophytic grassland within radii of 25 m; 50 m;... up to 250 m. Because of the correlation of percentages of different strata in different distances around the plots only one variable of this kind was included as a predictor in the analysis. After a first analysis yielding first insights into suitable habitats, we combined several categories of biotope types (e.g. proportion of suitable biotope types in a radius of 25 m, see Table 2).

Table 2: Habitat parameter measured in all sample plots resp. in the surrounding.

plot parameter	**unit / category**
biotope type	crop field / fallow land / intensively managed meadow / intensively managed meadow, meagre / extensively managed meadow / mesoxerophytic grassland / fringe vegetation, thermophile / hedges & bushes / oak forest, thermophilic / forest, without thermophilic oak forest
type of management	mown grassland / mown pasture / cattle grazed meadow / sheepherding / fallow land / mulched area
time of first annual management	until 15th June / until 15th July / until 15th August / after 15th August / fallow
inclination	[°]
sine exposition	[1]
cosine exposition	[1]
scale of shading	unshaded / partly shaded / largely shaded
cover value of bush encroachment	cover [%] (single bushes outside hedges)
height of bush encroachment	[m]
edge species	present / absent
hedge length	[m] (incl. hedges 2.5 m distant from sample plot)
hedge height	[m] (incl. hedges 2.5 m distant from sample plot)
hedge %	cover [%]
forest length	[m] (incl. forest 2.5 m distant from sample plot)
forest %	cover [%]
cover value of tree layer %	cover [%]
height of tree layer	[m]
cover value of shrub layer	cover [%]
height of shrub layer	[m]
cover value of lower herb layer	cover [%]
height of lower herb layer	[m]
cover value of upper herb layer	cover [%]
height of upper herb layer	[m]
cover value of moss layer	cover [%]
cover value of bare ground	cover [%]
Lotus corniculatus[1] %	cover [%]
Onobrychis viciifolia[1] %	cover [%]
Centaurea jacea[2] %	cover [%]
Centaurea scabiosa[2] %	cover [%]
Scabiosa columbaria[2] %	cover [%]
Knautia arvensis[2] %	cover [%]
Oreganum vulgare[2] %	cover [%]
surrounding parameter	**category resp. explanation**
suitable25	suitable biotope types concerning *Z. carniolica*: (= mesoxerophytic grassland, thermophilous fringes, extensively mown meadows) in a radius of 25 m.
MG/EMM100	mesoxerophytic grassland and extensively mown meadows in a radius of 100 m.
shareH25	share of hedgerows among suitable area concerning *C. arcania* in a radius of 25 m (suitable area = mesoxerophytic grassland, extensively mown meadows, thermophilous fringes, hedges).

[1] larvae food plants resp. [2] nectar plants of *Z. carniolica*

Based on a digital terrain analysis, Schröder et al. (2004) have quantified exposition, inclination and potential insolation for the entire research area. Furthermore the variables "cluster size" and "radius of gyration" (characterizing habitat patch size) were calculated in GIS. This was based on developed habitat suitability maps within the framework of habitat connectivity analysis (according to Keitt et al. 1997, see below). All these parameters have likewise been included in the present habitat model analysis. Therewith, it was also possible to investigate the influence of terrain parameters as well as the effect of habitat size and spatial configuration of habitat quality on the species' occurrence. For the incidence recording all adults of the two species encountered in 30 x 30 m^2-plots during a 15 minutes period (2 transect walks per sampling occasion) have been registered under optimum weather conditions (Pollard et al. 1975, Hermann 2000) within their main flight periods.

Statistical analysis

Construction and evaluation of the habitat models

As habitat selection of species takes place at different spatial scales (Luck 2002, Oppel et al. 2004, Wiens et al. 1987) and as we also aimed to predict species distribution for the whole research area, we developed habitat models on three different levels: a) plot models based on the parameters collected at the single plots (plot parameters), b) surrounding models which also includes information on the surrounding landscape (surrounding parameters) and c) area-wide models resp. DTM-area models, which are exclusively based on spatially available parameters (parameters on the surrounding or parameters of the digital terrain analysis, thus parameters of the terrain and the potential insolation) (see Table 2). Based on presence-absence data of the investigated species and the habitat characteristics of the study site, we use single and multiple logistic regression models to predict species occurrence (Manel et al. 1999a, Hosmer & Lemeshow 2000). First we start with a pre-selection of the predictors, as recommended by Hosmer & Lemeshow (2000). Biotope types without observations of individuals have been excluded from the analysis, as complete separation for some levels of categorical variables leads to inflated standard errors of the coefficients. For these eliminated strata we predicted a probability of occurrence equal to 0 %. If the lepidopterans have been present in 100 % of the cases, the biotope types have been combined with other strata (cf. Strauß et al. in prep.). The distribution of continuous predictor variables has been analyzed mainly by means of smoothed scatterplots (Hosmer & Lemeshow 2000). Clumped distributions (e.g. absence of middle cover values) have been coded into binary variables or variables with fewer categories, respectively (e.g. "tree

layer [%]" was coded binary "tree layer present/absent"). In case of unimodal relationships the squared term of the predictor variable was additionally taken into account. Extreme values have been omitted from the data set in some cases (Jongman et al. 1995). Based on likelihood-ratio-tests of univariate models, non-significant variables ($p > 0.2$) have been excluded from further analysis (Hosmer & Lemeshow 2000). To avoid multicolinearity, and thus a reduction of model reliability, we eliminated further habitat parameters from the analysis (Capen et al. 2001, Neter et al 1989). In case of strong correlation of variables only one of them was used (Spearman rank correlation $r_s > 0.5$; Fielding & Haworth 1995, Schröder 2000, Schadt 2002). The effect of the remaining explanatory variables on the response variable was evaluated by their odds ratios. This is a measure to estimate the effect of a predictor by specifying the ratio of odds between the presence or absence of a species during the explanatory variable value alter for one unit (Hosmer & Lemeshow 2000).
We performed a stepwise backward regression applying likelihood-ratio-tests to assess the significance of variables included in the model (Hosmer & Lemeshow 2000). Levels of significance have been $p_{in} = 0.05$ to include and $p_{out} = 0.10$ to exclude the variables (Adler & Wilson 1995, Schröder 2000). All statistical analysis have been performed with SPSS 11.0.
To evaluate the models we used R^2 of Nagelkerke (1991) to quantify model calibration. The discriminative power of the models was analyzed with AUC-values (Hanley & McNeil 1982, Zweig & Campbell 1993). According to Hosmer & Lemeshow (2000) an AUC-value of 0.7 was defined as a satisfactory level of discrimination, 0.8 as a good and 0.9 as a very good discrimination. Furthermore, Cohen's Kappa has been applied, as it is not negatively affected by the prevalence of species (Manel et al. 2001). Values exceeding 0.4 describe a clear, exceeding 0.6 a strong match between predicted and observed occurrences (Sachs 1999). As threshold for the discrimination between suitable and non-suited habitats (e.g. for habitat suitability maps) P_{kappa} was chosen, which represents the probability of occurrence when Kappa reaches the highest value (Fielding & Bell 1997, Schröder 2004). For the comparison of different alternative models we used the Akaike Information Criterion (AIC; Buckland & Elston 1993, Augustin et al. 2001).

Violation of model assumptions

An important assumption for regression analysis is the independence of samples (Hosmer & Lemeshow 2000). However, for variables of the landscape context the larger radii around neighboring plots partly overlap. In univariate models, the impact on model results is estimated by weighting the cases. While non-overlapping areas are weighted with 1, the weight of overlapping areas is reduced by half the degree of overlap (e.g. an overlap of 30% leads to a weight of 0.85 for both overlapping radii). The weighting procedure was conducted with an ArcView script developed by Strauß et al. (in prep.). Then the models with and without weighting have been compared using R^2_N-values. If only slight differences will be determined, we postulate a negligible impact on the models.

A further violation of model assumptions can be caused by spatial autocorrelation of the dependent variables (Legendre 1993, Fielding & Haworth 1995). In such a case, the nearer the sites are to each other, the higher the probability that they contain the same or very similar information. Thus they may not be independent (Lennon 1999, Smith 1994) and each observation may contribute less than one degree of freedom which is assumed in case of no autocorrelation (Legendre 1993). The resulting pseudoreplication (Guisan & Zimmermann, Heffner et al. 1996) may result in erroneous hypothesis tests and inferences. To test the extent to which spatial autocorrelation is inherent in our data, we calculated Moran's I for model residuals (Lichstein et al. 2002, Smith 1994). Analogously we also tested temporal autocorrelation between the two years of investigation. The incidence of the species of 2001 was used as explanatory variable for the model for 2002 and the AUC-values have been compared with those of the "original" model (vgl. Buckland & Elston 1993, Buckland et al. 1996, Schröder 2000). If the performance criteria changed for the better due to this predictor, one can assume temporal autocorrelation.

Habitat Model Validation

The models have been validated under different habitat conditions. To test model stability (Manel et al. 1999a) the models were developed with a partial data set and tested with the remaining data. We used a resampling technique with a tenfold cross-validation (Guisan & Zimmermann 2000, Schröder 2000). This helps to avoid that the model is too much adjusted to a specific data set and yields too optimistic performance criteria (Verbyla & Litaitis 1989, Reinecking & Schröder 2003).

To estimate the quality of predictions, the model has been transferred to independent data (Manel et al. 1999a) from the consecutive year (Dennis & Eales 1999) and from another research area (Schröder 2000). To test the quality of validation we used tests of model transferability according to Schröder (2000) applying significance tests of AUC-values (Beck & Shultz 1986) calculated along with their standard errors after applying the models to independent data sets. We regarded the evaluation as successful if the critical AUC-value threshold of 0.7 has been passed significantly (Schröder 2000).

Habitat suitability maps and habitat connectivity analysis

By applying the regression equation on maps of the spatial distribution of predictor variables (e.g. biotope types), we created habitat suitability maps of predicted occurrence probabilities (cf. Schröder 2000, Kleyer et al. 1999) for both species in the entire study area. The program code for the calculation of habitat suitability maps taking into account the landscape context was exemplary developed for *C. arcania* by Strauß et al. (in prep.).

Beside species distribution the habitat suitability maps act as the basis for a habitat connectivity analysis according to Keitt et al. (1997, see also Schröder 2000, Söndgerath & Schröder 2002). Depending on the spatial landscape pattern and the species specific dispersal ability, habitat patches may be functionally connected (With et al. 1997) to a habitat cluster, if the gap between suitable patches (threshold of habitat suitability p_{krit} is equivalent to P_{kappa}, see above) does not exceed a critical dispersal distance (d_{krit}, Keitt et al. 1997, van Langefelde 2000, Schröder 2000). The underlying threshold distances d_{krit} constitute 180 m for *Z. carniolica* (Holzschuh, pers. information) and 150 m for *C. arcania* (Höhfeld unpubl. data). These are mean values of individual maximum dispersal distances, determined in three study sites in the nature reserve "Hohe Wann" through mark recapture studies carried out in 2001. The mathematical representation of habitat connectivity is the correlation length (area-weighted mean radius of gyration), which can be interpreted as the mean distance a randomly placed species can move through the landscape before encountering a habitat edge (Keitt et al. 1997).

RESULTS

Effect of single environmental factors on incidence of study species

The prevalence of both species in the main study area remained rather constant in both years and was relatively high for *C. arcania*. While in 2001 29% of the plots have been occupied by *Z. carniolica* and 56% by *C. arcania*, the incidence in 2002 declined to 27% and 55%, respectively. In the validation area "Leutratal" *Z. carniolica* occurred on 32% und *C. arcania* on 72% of the study plots (Table 1).

Zygaena carniolica

We excluded farmland and forests from the analysis as definite „non-habitats". In another four biotope types no *Z. carniolica* adults have been found in 2001, however, because of their richness in nectar and larval foodplants these have been studied again in 2002.

The relationship between *Z. carniolica* occurrence and 13 independent variables was analysed further on (since $p<0.2$). Detailed results are presented in Table 3. They are based on the results of 2001 in the main study area. However, they are representative for all results of our study. Only the spectrum of biotope types with observations of *Z. carniolica* has been broader in 2002.

We observed the highest explanatory power for the variable „biotope type". The partly rather high odds ratios are to be explained by complete separation phenomena (i.e. only absences in specific biotope type) and are inflated. We can see the clear trend that *Z. carniolica* has the highest incidences in mesoxerophytic meadows, followed by thermophilous fringes and extensively mown grassland. This already became obvious in the frequency distribution of 2001, when mesoxerophytic meadows had 67% occupied plots, thermophilous fringes 46% and extensively mown grasslands 30%. In 2002, only single individuals of *Z. carniolica* have been found in the other biotope types (Table 1). Large proportions of the variation could be explained by the nectar plants (see R^2_N). The odds ratio is 8-fold compared with the absence of the plants for *S. colombaria*, 7-fold for *C. jacea*, and 4-fold for *K. arvensis*. The variable "moss layer" has a comparatively high R^2_N and affirmatively affects *Z. carniolica* occurrence, too. A 10% increase in hedgerow coverage leads to a 4-fold increase of the presence of the burnet. High values of R^2_N are also associated with "land use type". Compared to the odds ratio of fallow land, the probability of occurrence increases 5-fold for extensively sheep-grazed meadows and nearly doubles in the case of mown grasslands. Permanently grazed meadows, mown pastures and especially mulched areas have a negative impact on *Z. carniolica*. If we look at the time of first annual usage, a relatively late (after 15th August) as well as a relatively early date (before 15th July) is very suitable. In comparison to an early land use event (before 15th June) land use activities between the 15th of July and the 15th of August are rather negative.

Table 3: Univariate habitat model for *Z. carniolica* ("Hohe Wann", 2001): R^2_N and odds ratio of all significant predictor variables.

variable	p	R^2_N	category	odds ratio
biotope type	<0.0001	0.44	fallow land	reference category
			extensively managed meadow	11691
			intensively managed meadow / intensively managed meadow, meagre (combined category)	1.0
			hedges & bushes	1.0
			mesoxerophytic grassland	53959
			fringe vegetation, thermophile	22483
management type	0.004	0.20	fallow land	reference category
			mown grassland	1.8
			mown pasture	0.4
			cattle grazed meadow	0.5
			sheepherding	5.3
			mulched area	0.001
time of first annual management	0.041	0.01	until 15th June	reference category
			until 15th July	1.8
			until 15th August	0.7
			after 15th August	5.0
			fallow	1.3
inclination	0.143	0.03		1.3 (per 5°)
hedge % / hedge %^{2}	0.006	0.12		4.0 / 1.0 (per 10%)
edge species	0.033	0.05	absent	reference category
			present	2.6
tree layer height/ tree layer height ^{2}	0.102	0.05		2.2 / 0.9 (per m)
shrub layer % / shrub l ayer %^{2}	0.059	0.07		0.3 / 0.5 (per 10%)
herb layer %	0.124	0.03		0.2 (per 10%)
moss layer %	<0.0001	0.18		1.3 (per 10%)
Centaurea jacea	<0.0001	0.22	absent	reference category
			present	6.9
Scabiosa columbaria	0.001	0.12	absent	reference category
			present	8.3
Knautia arvensis	0.001	0.13	absent	reference category
			present	4.0

Furthermore, for *Z. carniolica* a highly significant ($p < 0.001$) variable of surrounding landscape was selected, which is a combination of the three suitable biotope types mesoxerophytic grassland, extensively mown meadow and thermophilous fringe. The coefficient of determination reaches its maximum considering a radius of 25 m around the plots (R^2_N = 0,47).

There is no significant relationship between the habitat connectivity parameters "radius of gyration" resp. "cluster size" and the occurrence of *Z. carniolica*.

The difference of R^2_N-values of the univariate models regarding the surrounding landscape with and without weighting for overlaps is only marginal and reaches the highest value of 0.06 for the parameter "fringes within a radius of 250m". For the variable "mesoxerophytic grassland, extensively mown meadow and thermophilous fringes in a radius of 25m", which was used for the model, the difference is only 0.001. Thus, the impact of overlaps of radii around neighboring plots is negligible even for large radii and we did not apply the weighting in these cases for further analysis.

Coenonympha arcania

We checked 12 explanatory variables (Table 4), with approximately half of them showing a strong relation to the occurrence of *C. arcania*.

Table 4: Univariate habitat model for *C. arcania* ("Hohe Wann", 2001)*:* R^2_N and odds ratio of all significant predictor variables.

variable	p	R^2_N	category	odds ratio
biotope type	<0.0001	0.25	fallow land	reference category
			intensively managed meadow	2.0
			intensively managed meadow, meagre	1.2
			extensively managed meadow	8.2
			mesoxerophytic grassland / thermophilous fringes / hedges (combined category)	15.0
inclination	<0.0001	0.23		2.1 (pro 5 Grad)
sine exposition	0.011	0.08		0.7 (pro 0.5)
cosine exposition	0.194	0.02		0.8 (pro 0.5)
scale of shading	0.045	0.05	absent	reference category
			partly present	2.4
time of first annual management	<0.0001	0.41	until 15th June	reference category
			until 15th July	4.3
			until 15th August	10.2
			after 15th August	55.0
			fallow	30.3
bush encroachment %	<0.0001	0.29		5.0 (pro 5%)
edge species	<0.0001	0.21	absent	reference category
			present	8.5
hedge %	<0.0001	0.31		13.5 (pro 10%)
tree layer	0.003	0.10	absent	reference category
			present	3.6
herb layer %	0.001	0.07		0.8 (pro 10%)
moss layer %	0.059	0.04		4.1 (pro 10%)

The by far highest explanatory power is yielded by the predictor "time of first annual management" (R^2_N = 0.41). Most positive is mowing time after the 15th of August, less so abandonment (or normally young fallows), and by far worse mowing dates between mid of July and mid of August. A high degree of explanation (R^2_N = 0.25) was found also with "biotope type". Here the combined category of mesoxerophytic grassland, thermophilous fringes and hedges yields the highest probabilities of occurrence of the species with 100% occupancy for thermophilous fringes and bush complexes. Since no butterfly was observed on farmland and forests we excluded these types from the analysis. An extremely strong relationship was found for parameters describing succession and marginal structures, where strong bush encroachment and a higher cover value of hedgerows reveal positive effects – the same holds true for the tree layer. Of the terrain parameters, there is the strongest relation to inclination. For every 5 degrees inclination we found a doubled probability of occurrence.

Among the parameters related to the surrounding landscape, the highest degree of explanation has been found with "share of mesoxerophytic grassland and extensively mown meadow in a radius of 100m" and with "share of hedgerows among 'suitable area' in a radius of 25m" ('suitable area'= thermophilous fringes, mesoxerophytic grasslands, hedges, and extensively mown meadows). Both variables show unimodal response curves (Fig. 1), where "share of hedgerows among 'suitable area' in a radius of 25m" within a range of 20 to 80% estimates 100% probability of occurrence and "share of mesoxerophytic grassland and extensively mown meadow in a radius of 100m" within 20 and 50% shows high values.

C. arcania's presence was not affected by the habitat connectivity parameters "radius of gyration" and "cluster size".

The univariate models of surrounding landscape with and without weighting for overlaps show hardly any difference (rarely R^2_N-differences are higher than 0.05). For the variable "share of mesoxerophytic grassland and extensively mown meadow in a radius of 100m" the difference is 0.01 and for "share of hedgerows among 'suitable area' in a radius of 25m" there is no difference in R^2_N-values. Again we postulate a negligible impact on the models.

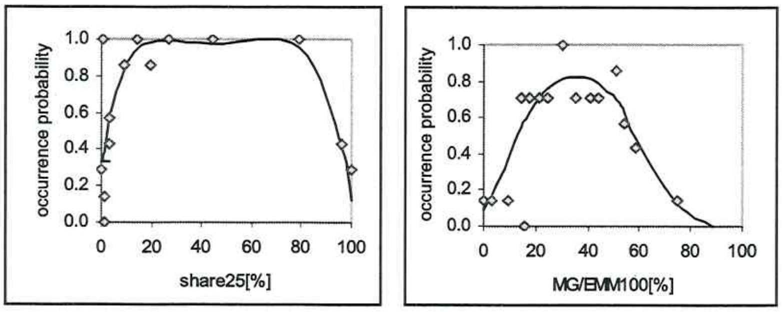

Figure 1: Response curves of univariate models considering the surrounding variables "shareH25" ("share of hedgerows among 'suitable biotope types' in a radius of 25m"; 'suitable biotope types' = thermophilous fringes, mesoxerophytic grassland, hedges, and extensively mown meadows) and "MG/EMM100" ("share of mesoxerophytic grassland and extensively mown meadows in a radius of 100m"). Rhombuses are the observed values (six values are each averaged).

Habitat models on different spatial scales

We could not find any spatial autocorrelation of the models of surrounding variables for the two species (Z = 0.547 as to *Z. carniolica*, Z = 1.010 as to *C. arcania*). But we registered temporal autocorrelation in our data. The information about the incidence of the butterflies in the previous year improved the model performance of the "original" plot models. AUC- and R^2_N-values increased from 0.86 to 0.93 (AUC) and from 0.47 to 0.66 (R^2_N) concerning *Z. carniolica*, resp. from 0.77 to 0.86 (AUC) and from 0.27 to 0.44 (R^2_N) concerning *C. arcania*. The habitat models of the different spatial scales and the respective performance criteria are shown in Tables 5 (*Z. carniolica*) and 6 (*C. arcania*).

Table 5: Cross-validated performance criteria of the final models for *Z. carniolica* in the nature reserve "Hohe Wann".

year	**model scale**	**modelparameter**	R^2_N	**AUC**	**Kappa**	P_{kappa}
2001	Plot model (Pc1)	biotope type, C. jacea, S. columbaria (AIC: 102)	0.57^1	0.86 [0.80 I 0.93]	0.57	0.47
	Surrounding model (Sc1)	*C. jacea, S. columbaria,* suitable25* (AIC: 94)	0.60^1	0.91 [0.86 | 0.96]	0.68	0.38
	Area-wide model (Ac1)	suitable25* (AIC: 108)	0.47^1	0.85 [0.79 | 0.92]	0.52	0.27
2002	Plotmodel (Pc2)	biotope type, *C. jacea, S. columbaria* (AIC: 111)	0.48^1	0.79 [0.65 | 0.86]	0.44	0.28
	Surrounding model (Sc2)	*C. jacea, S. columbaria,* suitable25* (AIC: 96)	0.47^1	0.84 [0.77 | 0.92]	0.55	0.38
	Area-wide model (Ac2)	suitable25* (AIC: 119)	0.28^1	0.75 [0.65 | 0.85]	0.41	0.28

[1] averaged value from the models of the ten-fold cross-validation

* suitable biotope types (= mesoxerophytic grassland, thermophilous fringes, extensively mown meadows) in a radius of 25 m.

Table 6: Cross-validated performance criteria of the final models for *C. arcania* in the nature reserve "Hohe Wann".

year	**model scale**	**modelparameter**	R^2_N	**AUC**	**Kappa**	P_{kappa}
2001	Plot model (Pa1)	management time_2, biotope type, hedge %, tree layer_present (AIC: 95)	0.65^1	0.85 [0.78 I 0.92]	0.64	0.50
	Surrounding model (Sa1)	management time_2, tree layer_present, MG/EMM100^{+2*}, shareH25^{+2**} (AIC: 92)	0.71^1	0.90 [0.84 | 0.96]	0.66	0.63
	Area-wide model (Aa1)	MG/EMM100^{+2*}, shareH25^{+2**} (AIC: 97)	0.59^1	0.87 [0.80 | 0.94]	0.62	0.50
2002	Plot model (Pa2)	inclination, bush encroachment % (AIC: 116)	0.40^1	0.79 [0.71 | 0.88]	0.51	0.51
	Surrounding model (Sa2)	inclination, bush encroachment %, MG/EMM100^{+2*} (AIC: 110)	0.49^1	0.83 [0.75 | 0.91]	0.53	0.37
	Area-wide model (Aa2)	MG/EMM100^{+2*}, shareH25^{+2**} (AIC: 124)	0.38^1	0.76 [0.67 | 0.85]	0.39	0.63
	DTM-Area model (DAa2)	MG/EMM100^{+2*}, shareH25^{+2**}, inclination (AIC: 114)	0.48^1	0.82 [0.74 | 0.90]	0.55	0.58

[1] averaged value from the models of the ten-fold cross-validation

$^{+2}$ = variable is given both as linear and squared term

* mesoxerophytic grassland and extensively mown meadows in a radius of 100 m.

** share of hedgerows among suitable area (= mesoxerophytic grassland, extensively mown meadows, thermophilous fringes, hedges) in a radius of 25 m.

Zygaena carniolica

On the level of plots, only biotope type and binary presence of nectar plants *Scabiosa columbaria* and *Centaurea jacea* remain in the model as these variables best fulfill the performance criteria of the models (Table 5: plot model Pc1). If additionally the variable of surrounding vegetation is considered, the AUC-value changed for the better and the variable biotope type drops out of the model (Table 5: surrounding model Sc1). With increasing percentage of suitable area (mesoxerophytic grasslands + extensively mown meadows + thermophilous fringes) within a radius of 25 m ("suitable25") and with the presence of nectar plants, the occurrence probability increases drastically (Fig. 2). Even with a 100% area of suitable biotope types, the presence of the burnets is estimated to be only 30% if the nectar plants are excluded. On areas with at least 50% suitable biotope types and available nectar sources the probability again increases clearly up to 85%. If only "spatial parameters" (surrounding parameters and parameters of the digital terrain analysis) are used for model building, only the variable of the surrounding vegetation remains in the model (Table 5: area-wide model Ac1).

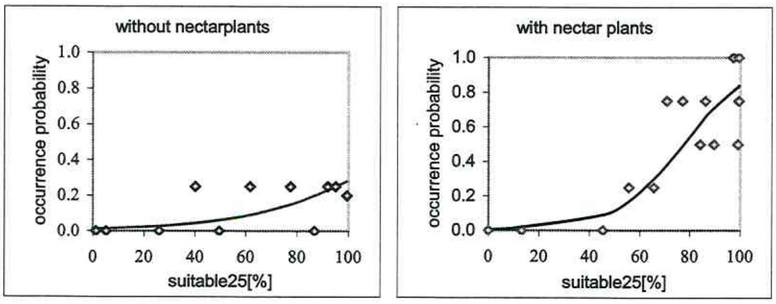

Figure 2: The response curve of the *Z. carniolica* model consisting of plot and surrounding parameters (Sc1) show the occurrence probability depending on the proportion of suitable area within a radius of 25 m: r.h.s nectar plants present, l.h.s without nectar plants. Rhombuses are the observed values (six values are each averaged).

All three models are well calibrated indicating a strong relation between observed and predicted values. After applying the cross-validation the discriminative power of the models remains very high, indicating a high robustness of the models. As expected, the model of surroundings which integrates variables of the sites as well as their surroundings reaches the highest precision. Because of the omission of the categorical variable "biotope type" less degrees of freedom are used, so that the AIC-value is improving.

In the model transfers, the AUC-values only slightly deviate from the original models. All *Z. carniolica* models remain significant after temporal as well as spatial transfer ($p<0.01$).

If habitat models are made for the Hassberge data set of 2002, exactly the same variables are selected for model construction, with slightly reduced model performance (see Table 5: Pc2, Sc2, Ac2).

Coenonympha arcania

The model for *C. arcania* which performs best (Table 6: plot model Pa1), integrates the variables "time of land use", "biotope type", "percentage of hedgerows", and the binary variable "tree layer present". As the regression coefficients of the categories of early and late land use (incl. fallow) are very similar, the variable "time of land use" was coded in a binary way with the two categories "until 15th of July", respectively "after 15th of July". This leads to a drastic improvement of the AIC-values due to the decreased number of parameters.

If the variables related to the surroundings are included in the model (Table 6: surrounding model Sa1), the variables "biotope type" and "percentage of hedgerows" drop out. The model is shown in Fig. 3. In each partial diagram the probability of occurrence is plotted against the two variables of the surrounding (shareH25, MG/EMM100). In the left column the probability of occurrence is shown if the tree layer is absent, in the right one if it is present. The lines depict different times of first land use. The threshold value p_{kappa} constitutes 0.70. A late management and the presence of a tree layer have the strongest positive effects. Optimum habitat patches of *C. arcania* have a percentage of hedgerows between 20 and 80 among "suitable area" in the direct surroundings and 10 - 60% of mesoxerophytic grassland and extensively mown meadows within a radius of 100 m. Late first land use and the presence of a tree layer even enlarge this span of optimum conditions.

In the area-wide model, the variable biotope type is skipped and the only remaining ones are the two variables considering the surroundings (Table 6: area-wide model Aa1). The inclusion of the terrain variable "inclination" yields an additional improvement of the model (Table 6: DTM-area model DAa1).

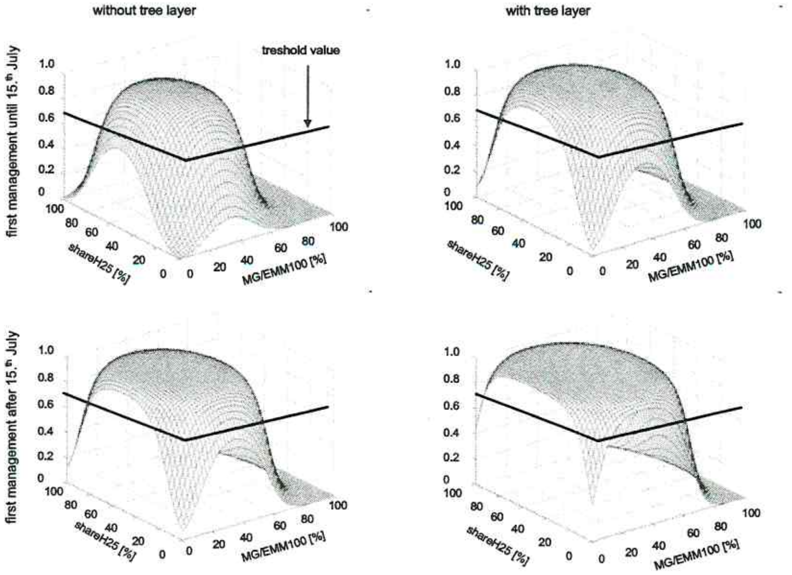

Figure 3: The response curve of the *C. arcania* model consisting of plot and surrounding parameters (Sa1) show the occurrence probability (z-axis) depending on both surrounding parameters (MG/EMM100: x-axis, shareH25: y-axis). R.h.s without, l.h.s. with present tree layer resp. above with an early point in time of management in the year and below with a late annual management.

The models for *C. arcania* are characterized by a good calibration and an extremely good discrimination after cross-validation. On all spatial scales the habitat models are robust. For this species again, the model of the surroundings has the highest level of performance. While the models are perfectly transferable in time ($p<0.001$), a significant spatial validation was not possible for *C. arcania*.

Within the Hassberge data set of 2002 only the variables "inclination" and "bush encroachment" remain (Table 6: Pa2). If neighborhood conditions are additionally included the variable "share of mesoxerophytic grassland and extensively mown meadow in a radius of 100m" is selected (Table 6: Sa2). The habitat models for the prediction of occurrence probabilities for the entire research area are identical with those of 2001 (Table 6: Aa2 and DAa2). Performance criteria of the 2002-models are a bit lower, but indicate a good calibration and discrimination even after cross-validation.

Habitat suitability maps for area-wide prediction of the species of interest and habitat connectivity analysis

We estimated habitat suitability maps for the entire nature reserve "Hohe Wann" based on the area-wide models, considering explanatory variables for which maps were available that cover the whole study area. To discriminate between suitable habitat patches and non-suitable matrix we applied a threshold occurrence probability that maximizes Cohen's kappa - P_{kappa} (cf. Schröder 2004). For *Z. carniolica* P_{kappa} was 0.22 and for *C. arcania* the P_{kappa} was 0.57. In total we predicted *Z. carniolica* to occur in nearly 7% of the whole study area investigated. Nearly half of these patches reached probabilities of occurrence exceeding 50%, with a maximum at 66%. The proportion of suitable *C. arcania* habitats was nearly three-fold (18%), with a probability exceeding 80% on 15% of the patches.

A connectivity analysis yielded 28 clusters (or „isolated" habitat patches) for *Z. carniolica* and 10 clusters for *C. arcania*. The analysis was based on the landscape pattern and the critical dispersal distance d_{krit} (mean flight distance in three sub-areas: 180 m for *Z. carniolica* and 150 m for *C. arcania*) at a grain size of 25m (see Figs. 4 and 5). As a measure of habitat connectivity we calculated the correlation lengths (Söndgerath & Schröder 2002) yielding C = 693 m for *Z. carniolica*, and C = 649 m for *C. arcania*. Based on the maximum proven flight distances among these three sub-areas (*Z. carniolica* 1850 m and *C. arcania* 2400 m), all habitat patches are potentially connected.

Figure 4: Binary habitat suitability map with p_{krit} = 0.22 (l.h.s) and habitat cluster map with d_{krit} = 180 m (r.h.s.) for *Z. carniolica* in the nature reseve "Hohe Wann". The individual clusters are variedly coulored in greyscales. Lines represent the "functional linkage" inside a cluster.

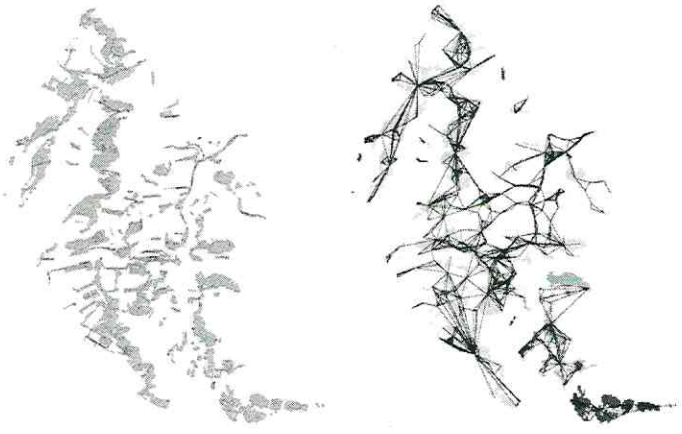

Figure 5: Binary habitat suitability map with $p_{krit} = 0.57$ (l.h.s) and habitat cluster map with $d_{krit} = 150$ m (r.h.s.) for *C. arcania* in the nature reseve "Hohe Wann". The individual clusters are variedly coulored in greyscales. Lines represent the "functional linkage" inside a cluster.

DISCUSSION

Habitat models in the landscape context

Zygaena carniolica

In both study areas *Z. carniolica* shows a clear preference for mesoxerophytic grassland, followed by thermophilous fringes and extensively mown meadows. Singular encounters of the burnet in otherwise unsuitable habitats can be traced back to available nectar sources. Accounting for the presence of *Centaurea jacea* and *Scabiosa columbaria* tremendously improves the predictive performance of the models for *Z. carniolica*. The predicted distribution of *Z. carniolica* matches literature information very well (Ebert & Rennwald 1994, Weidemann & Köhler 1996, SBN 1997, Kreusel & Böhmer 1998), where the species is characterized as typical representative of xerophytic and mesoxerophytic grasslands (Weitzel 1982). Besides being a nectar source the high importance of the nectar plants also seems to be related to the aggregation behaviour of the species. The latter is discussed as a strategy to find mates and to minimise predation risk (Ebert & Rennwald 1994, Krebs 1998). Among the nectar plants only *Centaurea jacea* and *Scabiosa columbaria* remained as significant predictor variables, all other nectar plants did not significantly improve the model and thus were skipped. Although the preference for nectar plants might vary geographically as well as phenologically (e.g. preference for *Knautia arvensis*, Smolis & Gerken 1987 and

Kreusel & Böhmer 1998), the presence of *C jacea* and *S. columbaria* seems to be sufficient to predict the incidence of *Z. carniolica* in other regions. This was shown in the control area "Leutratal".

According to Thomas et al. (1992), habitat requirements of most insect species are especially driven by the larvae rather than the adults. This however does not hold true for *Z. carniolica*. The low influence of larval food plants is most probably due to the presence of *Lotus corniculatus*, i.e. the larval food source in the investigation area, which is widespread and thus not limiting (B. Reiser, pers. comm.). It can be questioned whether the model would yield comparable predictive performance in areas where the (at least locally) much rarer *Onobrychis viciifolia* is used as food resource (Ebert & Rennwald 1994). But also Cowley et al. (2001) found better results for Lepidoptera habitat models based on the habitat composition rather than solely the presence of larval food plants. This was particularly true for species with strong habitat links which can hardly be encountered in unsuitable habitats but which are extremely abundant and widespread in suitable ones. Such characteristics are also reported for *Z. carniolica* (Smolis & Gerken 1987, Ebert & Rennwald 1994, Kreusel & Böhmer 1998).

The significantly positive relationship between percentage of hedgerows and the incidence of *Z. carniolica* might be explained with a lee effect (and thus prevention of windy situations). However, this might also be explained indirectly, like in the case of moss cover. The higher incidence of adults in fact might be due to the low land use intensity of the preferred sites, which also leads to a high degree of bush encroachment and increased moss cover.

The habitat requirements of *Z. carniolica* in relation to land use correspond to the present knowledge (Ebert & Rennwald 1994, Weidemann & Köhler 1996, SBN 1997) but were defined more precisely now. An extensive sheepherding promotes the species, followed by hay meadow management, cattle penning, mown pastures and particularly mulched sites are extremely unsuitable. The first disturbance due to land use during the year should take place either rather late (after the 15th of August) or relatively early (before the 15th of July), because mowing seems to have a negative impact if applied during the main flight period of the adults i.e. between 15th of July and 15th of August.

According to our study, the presence of *Z. carniolica* is predominantly influenced by habitat quality in the direct surroundings of the patches. Inclusion of variables in larger radii did not lead to significant model improvements. The fact, that the connectivity parameter "cluster size" did not have any affect on *Z. carniolica* occurrence affirmed this hypothesis. Although, within radii up to 250 m distance there still is a positive (but decreasing) influence of suitable habitats. R^2_N decreases from 0.47 (25 m radius) continuously to 0.24 (250 m radius). This might be due to the species' dispersal behaviour. On the one hand it is regarded as extremely sedentary in different MRR studies (Kreusel & Böhmer 1998, Holzschuh, pers. comm., Smolis & Gerken 1987). On the other hand there are observations that *Z. carniolica* can fly for several kilometers partly across unsuitable habitat (Kreusel & Böhmer 1998, Hübner pers. comm., A. Holzschuh, pers. comm., own observations) and thus is able to colonise isolated habitats.

Coenonympha arcania

Coenonympha arcania was mainly observed in patches with comparatively late and extensive use (after the 15th of July or even better after the 15th of August), in fallow land, or irregularly used patches with a high cover of woody plants (hedges and trees). Ebert & Rennwald (1991) also mention a preference for neglected grassland, extensively mown meadows, thermophilous fringes and bush complexes and an influence of land use timing, as the species rarely occurs on unused patches and seems to prefer higher grass layers for oviposition (Ebert & Rennwald 1991, Feldmann et al. 2000). On early used patches the preferred nutrient poor grasses are missing. The optimum type of land use could not be assessed due to the limited data set. Further studies conducted in the same area (Höhfeld unpubl. data) on patches with a high structural diversity and different land use regimes were not able to identify any preference of specific land use types. Ebert & Rennwald (1991) speculate that the species is particularly sensitive to fertilisation and mowing. SBN (1991) recommends partial mowing or low intensity grazing, as a strong bush encroachment or succession also may pose a threat to the species. In the (thermophilous) forests covering parts of the research area we did not encounter any *C. arcania* adults. Pre-forest stages as well as forest margins however are inhabited by the species (Ebert & Rennwald 1991, Feldmann et al. 2000). Bink (1992) states a preference for ecotones between open land, hedges and forest margins due to more balanced microclimatic conditions which is favored by the species. The high percentage of woody elements found in the preferred biotopes confirms this assumption. Furthermore, shrubs are used for territorial behavior and sun basking (Ebert & Rennwald 1991), which might explain the positive influence of succession (see also Ebert & Rennwald 1991, Höhfeld unpubl. data), which is more pronounced on shrub rich and thus extensively used patches. The preferred larval food plant *Brachypodium pinnatum* (Hermann pers. comm.) typically grows in mesoxerophytic meadows (Oberdorfer 2001). Within the research area steeply inclined hills are preferred habitats of *C. arcania* (cf.

habitat suitability map). This preference most probably again reflects the low land use intensity rather than the relative unsuitability of less inclined patches. Single specimens have indeed been encountered in flat areas with suitable vegetation structure.

The unimodal response curve, i.e. a maximum habitat quality for mean values of the predictor variable, of both variables of the surroundings clearly shows the strong link of *C. arcania* to a biotope complex. An extended area of shrubs without a nutrient poor margin reduces butterfly density as does nutrient poor grassland without any shrubs. This fits into the general characterization of the species as limited to mosaic-structured landscapes (Bink 1992). Beneath the percentage of hedgerows within suitable habitat in the direct surrounding also nutrient poor grasslands within 100 m around the patch strongly positively influence the incidence. Patches in larger distances seem to have low impact on the presence of *C. arcania*, most probably because of the butterfly's home range. Within the MRR study of Höhfeld (unpubl. data) most adults only reached home ranges between 100 and 150 m. This corresponds to Bink (1992), who states area requirements for a population of *C. arcania* of approximately 4 ha (which equals a radius of 110 m). Biotope combination plays a minor role in larger distances, although individuals might be able to reach distant and isolated patches (up to 2 km distance; Höhfeld unpubl. data). The insignificance of the variable cluster size on this species likewise justifies this assumption.

The best habitats of *C. arcania* are large complexes of extensively mown meadows and mesoxerophytic grasslands with thermophilous fringes (within a radius of 100 to 150 m), with at least locally high shrub cover (up to 80%). Patches with irregular or late land use (after mid July) as well as presence of single trees increase the probability of occurrence.

Both species have neither been found on arable land nor in any type of forest, although forested patches are sometimes mentioned as habitats in the literature (see above). For future investigations we therefore recommend pilot studies to clearly identify the unsuitable habitats and thus increase the number of samples in relevant biotope types (compare Hirzel & Guisan 2002). Although the recommended sample size of Morrison et al. (1998) of at least 25-30 samples per predictor variable has been reached for nearly all models, a higher number would have been partly desirable for *C. arcania*.

The problem of overlapping radii around neighboring sample sites was reduced – but not completely eliminated - by lumping suitable biotope types. However, violating the assumption of independence of samples in these respective models did not lead to significantly higher performance criteria (R^2_N-values). Thus, inclusion of all sample sites for the analysis of the landscape context seems justifiable. Alternatively the maintenance of a certain minimal distance between sites would have been possible, as recommended by Legendre (1993) to avoid spatial autocorrelation. We did not find spatial autocorrelation in the residuals of the models for both species. The presence of *Z. carniolica* and *C. arcania* is however strongly correlated in time, due to their high site fidelity. In both years they inhabited nearly identical patches. The same phenomenon (temporal autocorrelation) was found by Schröder (2000) for the grasshopper *Stetophyma grossum*, while the inclusion of the variable "presence in the previous year" in the case of *Conocephalus dorsalis* did not yield any model improvement. In an equivalent situation regarding the bird species *Motacilla flava* and *Anthus pratensis* Schröder (1999) gained better results applying the dichotomous variable "breeding site in the previous year" than with the best models based upon the habitat parameters assessed. In the case of high territorial and site fidelity there will even be no temporal independence after many years. This also gives the possibility to use the variables of autocorrelation to predict the presence of species (Buckland et al. 1996).

Model validation

The models of *Z. carniolica* were very stable, i.e. the same predictor variables were selected in different years and could be easily transferred in time and space. In case of *C. arcania*, other variables were selected in the second year. The parameters inclination and bush encroachment seem to replace the variables of the 2001 model, as they integrate specific habitat conditions (see above). A significant spatial validation however could not be performed in the Leutratal area, which might be due to the low number of sampling sites (n = 18) and the low variability of habitat conditions regarding management and inclination. Here, the problem seems to be more one of different study designs than a lack of transferability, as Hein et al. (in prep.) showed for orthopterans in nearly the same sites in the Leutratal area (compare Lehmann et al. 2002).

Implications for nature conservation

Our results show, that simple models - taking into account only a few predictor variables - yielded good to very good predictive performances for both species. We applied models considering the percentage of biotopes only to calculate habitat suitability maps for the whole nature reserve "Hohe Wann". Thereby this information is available in terms of vegetation or biotope maps for many regions. Since our models are validated in space and time and due to the concordance to literature information on the habitat requirements of these species, one can adopt, that the models will yield reliable predictions also for other regions with similar biotope configurations and comparable management regime in a relatively fast and cost-effective manner. Therefore these habitat models are highly relevant for species and nature conservation.

The probability of occurrence of a species is also determined by population dynamic factors in addition to habitat quality. In our approach population dynamic factors could not be considered because of the static characteristic of habitat modeling (Gustafson 1998). However, taking into account the estimated habitat suitability maps as well as the results of mark recapture studies (unpupl. data) we carried out a habitat connectivity analysis that extracts information about the effect of isolation and patch size, which may influence butterfly occurrence in addition to habitat quality (Thomas et al. 1992, 2001, Hanski & Gilpin 1997, Wahlberg et al. 2002). This analysis considers the spatial arrangement of the landscape elements, which significantly influences species' occurrences (e.g. Collinge 1998, Kuhn & Kleyer 1999b, Guiterrez et al. 2001, Thomas & Hanski 1997, Schröder 2000). Our results show, that neither cluster size nor radius of gyration play a significant role for the two species. However, in this context, we have to consider the scale in which the organisms interact with the landscape patterns (Blaschke 1999, van Langevelde 2000, Eon et al. 2002). On a comparative small spatial level (radii of 200 to 250 m at maximum) the focal species may be affected by the area of suitable habitats. However, a negative impact of small patch sizes on butterfly presence could not be verified, probably because of the relative high amount of high-quality habitat in the whole nature reserve „Hohe Wann“. The mean cluster size constitutes 9 ha for *Z. carniolica* and 105 ha for *C. arcania*. This values exceed the estimated minimum patch size of both species (see Smolis & Gerken 1987, Bink 1992). The missing influence of isolation and habitat configuration on patch occupancy may also be due to the high habitat quality for both species. In addition, there is a high degree of connectivity for both species between the suitable patches, if d_{krit} is based on the maximal proven flight distances of the three studied sub-sites. A closely linked habitat network among all subpopulations is extremely likely (as indicated by single dispersal events). In a relatively small part of the study area (6.5 ha in *C. arcania* and 11.4 ha in *Z. carniolica*) dispersal flights of 1850 m were detected for *Z. carniolica* (Holzschuh, pers. comm.) and 2000 m for *C. arcania* (Höhfeld unpubl. data). Dennis & Eales (1997) state, that habitat quality and patch size are more influential factors for butterfly occurrence than isolation. But according to the same authors, wherever site extinction has progressed further, isolation is likely to be a more prominent factor. This assumption is confirmed by Krauss et al. (2004) for *C. minimus*: while isolation did not play an important role for patch occupancy in their very well-suited landscape. The distribution of this butterfly was clearly more scattered in comparatively suboptimal landscapes (Baguette et al. 2000) as e.g. also in our study area (Binzenhöfer et al., in prep. a).

Our results also demonstrate that our landscape is not inherently fragmented or connected. In spite of the lower dispersal ability (d_{krit}) of *C. arcania* in comparison to *Z. carniolica*, the habitat network of the former is considerably greater. Species distribution mainly depend on the vagility and ecological amplitude of a species (see also Wiens et al. 1997, Eon et al. 2002), and is therefore species and landscape specific (Tischendorf & Fahrig 2000). These aspects should be taken into account for nature conservancy and strategy.

CONCLUSIONS

In regions with high density of suitable biotopes habitat quality is the main important factor for patch occupancy of butterflies and moths. Even when the effect of isolation and habitat size on species occurrence is not detectable, the impact of the composition of habitats in the surrounding landscape may be significant. Therefore, investigations of habitat preferences should always be taken on different spatial scales (cf. Oppel et al. 2004).

Chapter III

The generality of habitat suitability models: How well may grasshoppers be predicted by butterflies?

Silke Hein, Birgit Binzenhöfer, Hans-Joachim Poethke, Robert Biedermann,
Josef Settele and Boris Schröder

IN PREP. FOR BASIC AND APPLIED ECOLOGY

Abstract
Knowledge of the relationship between habitat properties and the occurrence of a particular species is an essential prerequisite for the conservation of species. Habitat suitability models are one possibility to describe habitat preferences of a species quantitatively and objectively. In this study we compare the habitat preferences of different insect species (grasshoppers, bush crickets, butterflies, moths) in the same area and with the same methods. To identify common parameters to predict occurrence probability of these species, we first tested transferability of single species models to species within the same insect group. The 'best' group models were then tested for transferability between the different groups.

Although in the single species models different key factors have been shown to be responsible for habitat suitability, some models were successfully transferred. The habitat preferences of the moth *Z. carniolica* were particularly well suited for the prediction of suitable habitats for all other species. The variable 'type of biotope' played a dominant role in all models. With this predictor suitable habitat may be predicted for all studied species under different management regimes.

INTRODUCTION

Historically, arid grasslands arose due to anthropogenic influences, e.g. logging or abandonment of vineyards or fields on steep hill sides. In former times, they have most often been used as grazing sites or mowing areas. Situated mostly on nutrient poor soil or inaccessible hill sides they usually are of low agricultural productivity (Willems 1990, van Dijk 1991) and only worked with high effort. Nowadays these semi-natural habitats are increasingly lost by either intensification (e.g. through fertilisation) or abandonment (e.g. succession by shrubs and hedges; Mühlenberg et al. 1996, van Dijk 1991, Poschlod et al. 1996, Kahmen et al. 2002). But because these areas simultaneously accommodate a variety of threatened and protected animal and plant species (van der Maarel & Titlyanova, Kull & Zobel 1991, Bignal & McCracken 1996), it is a declared objective of nature conservation in Europe to protect them (Bobbink & Willems 1993, Söderström et al. 2001). However, management regimes for these areas are not easily developed since maintenance depends on regular management, but species diversity is known to decline with increased management intensity (Kruess & Tscharntke 2002). Thus, a variety of different management regimes has been proposed and tested (Schreiber 1977, Bakker 1989, Bobbink & Willems 1993, Kahmen et al. 2002) including the ones from the MOSAIK-project: rototilling and extensive grazing by goats (see Fritzsch et al. in prep., Kleyer et al. in prep.).

Independent of the kind of management and the time intervals between management events a certain vegetation composition or rather successional stage of the managed area can be found. This successional stage results in different levels of habitat suitability for different animal species. Which degree of succession will be advantageous for the desired 'target species' can be determined by describing the habitat requirements of a species with statistical habitat suitability models (Bonn & Schröder 2001, Hein et al. in prep.). Different species or insect groups vary in their respective habitat needs. Therefore the resulting favoured successional stage will vary from species to species.

For the conservation of grasslands it is important to protect as many species as possible. Thus, habitat requirements of a large number of single species have to be brought together. In this context one could imagine two approaches. First, the identification of single species which are representatives for others concerning habitat requirements (New 1995, Simberloff 1998, Bonn & Schröder 2001). Secondly, the combination of single species habitat requirements to find a common set of variables relevant for the occurrence of a maximum number of species. Both methods would make it feasible to predict suitable habitats and the impact of different management types on the occurrence of more than one species.

Within the MOSAIK project the habitat requirements of different insect species have been studied separately (Binzenhöfer et al. in prep. a, b, Hein et al. in prep., Strauß et al. in prep.). In this study we compare results of these analyses for three different Orthoptera (Ensifera: *Metrioptera bicolor*, *Platycleis albopunctata*, Caelifera: *Stenobothrus lineatus*) and two butterfly species (Lepidoptera: *Coenonympha arcania*, *Zygaena carniolica*) typically found on semi-arid grasslands and tested whether the inclusion of factors delivered by a digital terrain model and a landscape model (see Schröder et al. in prep.) increases their predictive power. For the resulting single species models we will first test transferability within the species of one insect group (within group transfer). The resulting 'group' models are then transferred to the other groups (between group transfer; Bonn & Schröder 2001). Additionally, for the determination of a representative or 'umbrella' species we tested whether the incidence of one species can be used to predicted incidences of others just as well (Hanley & McNeil 1983, Bonn & Schröder 2001).

MATERIAL AND METHODS

This study is based on data from different authors (Binzenhöfer et al. in prep. b, Hein et al. in prep., Strauß et al. in prep.). All studies used the same experimental design to achieve comparable data sets for the different species. To keep this section short, we would like to refer to the original papers for a detailed description of data collection and characterization of the experimental plots (Binzenhöfer et al. in prep. b, Strauß et al. in prep., Hein et al. in prep.). In cases were analyses differed in the original papers we adjusted all analyses to the methods presented in Binzenhöfer et al. (in prep. b) and Strauß et al. (in prep.).

The species

Grasshoppers and bush crickets

The stripe-winged grasshopper *Stenobothrus lineatus* (PANZER 1796; Orthoptera: Acrididae), the two-coloured bush cricket *Metrioptera bicolor* (PHILIPPI 1796; Orthoptera: Tettigoniidae) and the grey bush cricket *Platycleis albopunctata* (GOEZE 1778; Orthoptera: Tettigoniidae) are classified as thermo- and xerophilic (Harz 1969, Detzel 1998, Ingrisch & Köhler 1998). They typically inhabit arid and semi-arid grasslands as well as broom and juniper heath. *S. lineatus* and *P. albopunctata* are also found on fringes and areas with open soil and sparse vegetation. In contrast *M. bicolor* is more orientated towards vertical structures and thus prefers long lawn biotopes. For *S. lineatus* sheep-grazed areas and short vegetation structure are preferred habitat elements (Detzel 1998). In general, *P. albopunctata* has a more narrow distribution in Germany than the other two species.

Butterflies and moths

The flight period of the Pearly Heath *Coenonympha arcania* (LINNAEUS 1761; Lepidoptera: Nymphalidae) lasts from end of May till beginning of August. Generally this species is univoltine (Ebert & Rennwald 1991, Hensle 1995). Imagines are found on mesoxerophytic grasslands with bushes in the near vicinity of hedges and forest edges (Ebert & Rennwald 1991, Weidemann 1995, Settele et al. 1999). Caterpillars feed preferentially on *Holcus lanatus*, *Brachypodium pinnatum*, *Festuca ovina* or *Melica spec.* (Ebert & Rennwald 1991, Weidemann 1995).

The day active moth *Zygaena carniolica* (SCOPOLI 1763; Lepidoptera: Zygaenidae) has a flight period of four to five weeks from the end of June to mid August (Ebert & Rennwald 1994). This xerothermophilic species (Ebert & Rennwald 1994) inhabits mainly fallow as well as extensively grazed or mowed mesoxerophytic grasslands (Ebert & Rennwald 1994, Weidemann & Köhler 1996). Preferred caterpillar feeding plants are *Onobrychis viciifolia* and *Lotus corniculatus*. Imagines prefer purple flowering nectar plants like *Knautia arvensis*, *Scabiosa columbaria* and *Centaurea spec.* (Ebert & Rennwald 1994, Weidemann & Köhler 1996).

Field work

All studies were conducted in the field seasons of 2001 and 2002 in the nature reserve 'Hohe Wann' in Northern-Bavaria, Germany (latitude 50° 03′, longitude 10° 35′). The study area is characterised by abundant sites of mesoxerophytic grasslands, formerly used as vine yards (Elsner unpubl. data). These patches are separated by agricultural landscape of different use. The whole area covers approximately 10 km in NS-direction and 4 km in EW-direction.

Incidence of the species under study was recorded on 146, 139 and 106 experimental sites for orthoptera, *Z. carniolica* and *C. arcania* respectively. Experimental plots were selected by stratified random sampling across the ten main types of biotope occurring in the region. To increase the resolution of the logistic regression models we sampled with high effort in habitats with - based on prior knowledge – uncertain status regarding the species' occurrence (i.e. different kinds of open grasslands). To assure comparability of results the study plots of the grasshoppers and bush cricket studies (15 m x 15 m) were always a randomly chosen corner of the butterfly/moth plots (30 m x 30 m). Different plot sizes were chosen as butterflies/moths are more mobile than grasshoppers or bush crickets.

For the determination of grasshopper, bush cricket, butterfly and moth incidence we carried out transect sampling on the experimental sites. The census was terminated (i) as soon as a specimen was found or (ii) after a maximum of 15 minutes (butterflies, moths) or 20 minutes (grasshoppers, bush crickets) of sampling time. As the activity of grasshoppers, bush crickets, butterflies and day active moths strongly depends on weather conditions, censuses were only carried out during 'good' weather condition (sunshine, cloud cover < 3/8; air temperature > 17 °C; wind speed < 4 m/s (Mühlenberg 1993) to ensure the same detection probability on all plots.

Statistical analyses

Single species models

We used single and multiple parameter logistic regression to determine the impact of 'landscape' factors delivered by the digital terrain model and landscape model (like solar radiation, slope, soil type, geology, Schröder et al. in prep.) on the occurrence probability of all studied insect species (Manel et al. 1999a, b, Hosmer & Lemeshow 2000). For the selection of adequate models we started with an univariate analysis to assess indiviudal model variables independently from each other (Hosmer & Lemeshow 2000). To choose uncorrelated parameters for the development of multiple parameter models we calculated all pairwise Spearman rank correlations and selected only one variable of those pairs showing severe correlation ($\rho_s \geq 0.5$; Fielding & Haworth 1995, Schröder 2000). Only parameters with p-values < 0.2 (Hosmer & Lemeshow 2000) were included into multiple analyses.

For model evaluation we used Nagelkerkes R^2 value (Nagelkerke 1991, Harrell 2001). Model discrimination was assessed by the threshold independent AUC-value, i.e. the area under the receiver operating characteristic curve (ROC-curve), the (Hanley & McNeil 1983, Hosmer & Lemeshow 2000, Schröder 2000, Manel et al. 2001). Variables with an AUC-value > 0.7 were included into the models from the single species studies and their importance was tested with the stepwise backwards elimination procedure.

For comparison of the resulting models with the same dependent variable we used the Akaike Information Criterion (AIC, see also Buckland et al. 1997, Augustin et al. 2001), which allows to choose the model with the optimal compromise between goodness of fit and the lowest number of parameters. Models with the lowest AIC were tested for spatial autocorrelation by calculating Moran's I as an index of covariance between different point locations (Lichstein et al. 2002, Karagatzides et al. 2003). Only models without spatial autocorrelation were used for further analyses and internally validated by applying a bootstrapping procedure (Verbyla & Litvaitis 1989, Reineking & Schröder 2003). For internal validation we first calculated the AUC value of the full model with 300 bootstrap samples and then tested for stability of the model with variable selection by using the backward stepwise approach with $\alpha = 0.05$ and 300 bootstrap samples (see also Oppel et al. 2004).

Test of transferability

Each of the single species models was tested for transferability in two ways. First, the model was computed for the species it was developed for. Then predicted occurrence probabilities for that species were used to predict the occurrence of the other species (Hanley & McNeil 1983).

Secondly, we tested transferability by using the parameters from the 'best' model for species A and calculating a new model with these parameters based on the incidence of species B. In both cases agreement between predictions and occurrences are tested by comparing the AUC value with an $AUC_{crit} \geq 0.5$ (Schröder 2004). The transfer quality of a model is best when all possible combinations result in significantly better AUCs than 0.5. For *within group* comparisons of transferability this methods result in five possible combination for the three orthoptera species, respectively in three combinations for the two butterfly species. The highest possible number of successful transfers of a single species model for *between group* comparisons is seven.

The 'type of biotope' or derivates of this parameter were included in all single species models. Additionally, this parameter is landscape wide available. Thus, we tested the 'type of biotope' of the experimental plot of grasshopper and bush cricket incidences, which corresponds in most cases to the main type of biotope on all experimental plots, for its prediction ability. Thereby, its transferability was tested between species (25 possibilities for combination).

RESULTS

Single species models

The univariate analyses of the 'landscape' factors from the digital terrain and the landscape model (Schröder et al. in prep.) resulted in an influence of slope, solar radiation, disturbance intensity, management, geology and soil type on the occurrence probability of grasshopper, bush crickets and butterfly species. For the studied butterfly species, the grasshopper *S. lineatus* as well as for the bush cricket *M. bicolor* inclusion of these parameters in the so far best single species models did not result in new models as the parameters were eliminated during stepwise backward procedure (Table 7). Only for the bush cricket *P. albopunctata* inclusion of the parameter 'solar radiation' resulted in new models with lower AIC than the one presented by Hein et al. (in prep.; Table 7).

Table 7: Single species models with model characteristics (AUC with SE, R^2_N, AIC, $AUC_{bootstrapped}$ after internal validation with backwards variable selection) for the five investigated species ($p < 0.05$).

species	**model parameter**	**AUC**	**R^2_N**	**AIC**	**$AUC_{bootstrapped}$**
S. lineatus	type of biotope vegetation height (quadratic term)	0.762	0.367	115.92	0.735
M. bicolor	suitable habitat in radius = 50 m (i.e. fringes, mesoxerophytic grassland, extensively managed meadows)	0.740	0.227	117.94	0.723
P. albopunctata	sinus exposition vegetation height solar radiation proportion fringes in radius = 75m	0.949	0.712	40.84	0.941
C. arcania	time of first management incidence tree layer proportion mesoxerophytic & extensively managed grassland in radius = 100m proportion hedges on suitable area in radius=25m	0.94	0.7	92	0.9
Z. camiolica	incidence *Centaurea jacea* incidence *Scabiosa columbaria* suitable types of biotope in radius = 25m (i.e. fringes, mesoxerophytic grassland, extensively managed grassland)	0.92	0.6	94	0.911

For all three orthoptera species the 'fringe vegetation' has the highest probability of occurrence followed by mesoxerophytic grassland. In addition, low vegetation height increases occurrence probability of *S. lineatus*. For *P. albopunctata* habitat suitability decreases with increasing vegetation height, increasing solar radiation and west faced exposition (Table 7).

The occurrence probability of *C. arcania* is positively influenced by late 'time of first management' and an existing 'tree layer' (Table 7). Additionally, a high 'proportion of mesoxerophytic grassland and extensively managed meadows in the radius of 100 m' and a high 'proportion of hedges on suitable habitat in the radius of 25 m' increase the occurrence probability of the species. The highest probability of occurrence for *Z. carniolica* is predicted for areas with a high proportion of mesoxerophytic grasslands, fringes and extensively managed meadows (indicated by the inclusion of the variable 'proportion of suitable habitat in a radius of 25 meter'). Additionally, the occurrence of *Scabiosa columbaria* and *Centaurea jacea* contributed to the model (Table 7).

Test of transferability

For grasshoppers and bush crickets transferability of a single species model *within group* was best conducted with the model of *S. lineatus* including the variables 'type of biotope' and 'vegetation height' (Table 8). The occurrence of *C. arcania* and *Z. carniolica* is best predicted by the model of *Z. camiolica* (Table 8). Hereby, the proportion of suitable habitat (fringes, mesoxerophytic grassland, extensively managed grassland) in a radius of 25 m as well as the occurrence of the sucking plants *Centaurea jacea* and *Scabiosa columbaria* are explaining variables in the model.

Table 8: Results of *within group* transfers. For orthoptera the model of *S. lineatus*, including the variables 'type of biotope' and 'vegetation height' showed the best transferability (five successful out of five possible transfers). For butterflies the model of *Z. carniolica*, including 'suitable habitat in radius = 25 m' and occurrence of *C. jacea* and *S. columbaria* was best transferable. AUCs significantly exceeding an AUC_{krit} = 0.7 are indicated by **, those significantly exceeding an AUC_{krit} = 0.5 by *. Original models are marked in grey.

independent variables from the model of species	species incidence used for model calibration	species incidence to be predicted	model outcome – transferability	
			AUC	lower...upper confidence bounds
S. lineatus	*S. lineatus*	*S. lineatus*	0.762*	0.677...0.848
		M. bicolor	0.632*	0.525...0.739
		P. albopunctata	0.870**	0.794...0.946
	M. bicolor	*M. bicolor*	0.771*	0.68.....0.862
	P. albopunctata	*P. albopunctata*	0.868**	0.788...0.948
Z. camiolica	*Z. camiolica*	*Z. camiolica*	0.919**	0.870...0.969
		C. arcania	0.613*	0.507...0.719
	C. arcania	*C. arcania*	0.898**	0.837...0.960

In the *between group* transfer the model of *Z. carniolica* performs slightly better than the one from *S. lineatus* (one more successful transfer; Table 9). The independent variable 'type of biotope' showed the highest transferability to all species, with 100 % (=25/25) successful transfers (Table 10).

Table 9: Results of *between group* transfer with the butterfly 'group' model (*Z. carniolica*). AUCs significantly exceeding an AUC_{krit} = 0.7 are indicated by **, those significantly exceeding an AUC_{krit} = 0.5 by *. Original models are marked in grey.

independent variables from the model of species	species incidence used for model calibration	species incidence to be predicted	model outcome - transferability	
			AUC	lower...upper confidence bounds
Z. carniolica	*Z. carniolica*	*Z. carniolica*	0.919**	0.870...0.969
		S. lineatus	0.760*	0.681...0.839
		M. bicolor	0.766*	0.681...0.839
		P. albopunctata	0.738*	0.650...0.826
	S. lineatus	*S. lineatus*	0.775*	0.688...0.862
	M. bicolor	*M. bicolor*	0.747*	0.659...0.835
	P. albopunctata	*P. albopunctata*	0.787*	0.674...0.9

Table 10: Results of tests of transferability with the independent variable 'type of biotope' from 15m x 15m experimental plots. AUC significantly exceeding an AUC_{krit} = 0.7 are indicated by **, those significantly exceeding an AUC_{krit} = 0.5 by *. Models representing a single species model are marked in grey.

independent variable	species incidence used for model calibration	species incidence to be predicted	model outcome - transferability	
			AUC	lower...upper confidence bounds
type of biotope	*S. lineatus*	*S. lineatus*	0.846**	0.787...0.904
		M. bicolor	0.802**	0.734...0.870
		P. albopunctata	0.846**	0.769...0.922
		Z. carniolica	0.803**	0.727...0.880
		C. arcania	0.711*	0.624...0.799
type of biotope	*M. bicolor*	*S. lineatus*	0.842**	0.780...0.904
		M. bicolor	0.806**	0.739...0.873
		P. albopunctata	0.842**	0.762...0.922
		Z. carniolica	0.807**	0.734...0.879
		C. arcania	0.736*	0.650...0.821
type of biotope	*P. albopunctata*	*S. lineatus*	0.807**	0.740...0.873
		M. bicolor	0.766*	0.693...0.839
		P. albopunctata	0.855**	0.785...0.925
		Z. carniolica	0.777*	0.696...0.859
		C. arcania	0.678*	0.589...0.766
type of biotope	*Z. carniolica*	*S. lineatus*	0.847**	0.785...0.910
		M. bicolor	0.803**	0.73.....0.877
		P. albopunctata	0.840**	0.773...0.906
		Z. carniolica	0.82**	0.754...0.887
		C. arcania	0.745*	0.659...0.831
type of biotope	*C. arcania*	*S. lineatus*	0.773*	0.692...0.854
		M. bicolor	0.762*	0.68.....0.845
		P. albopunctata	0.832**	0.756...0.907
		Z. carniolica	0.770*	0.696...0.844
		C. arcania	0.811**	0.741...0.880

DISCUSSION

Single species models

The univariate logistic regression analyses with the 'landscape' parameters derived from the digital terrain and landscape model (Schröder et al. in prep.) resulted in significant models for all species. But none of these parameters is included in the multiple parameter models for *S. lineatus*, *M. bicolor*, *Z. carniolica* and *C. arcania*. Only the occurrence probability of *P. albopunctata* increased significantly with the inclusion of the factor solar radiation in the multiple parameter logistic regression models. This is in agreement with the high temperature requirements of this species for egg and larval development. Based on this results one may conclude that disturbance factors like disturbance frequency or intensity have no influence on habitat suitability for our species. We consider this a very unlikely situation. Especially, adult butterflies are sensitive to changes in temperature, light and humidity levels, parameters that are often affected by habitat disturbance (Wood & Pullin 2002). We assume that this result is better explained by the fact that other factors already included in the models contain the effects of disturbance or other 'landscape' parameters. For example the type of biotope may be such a factor, e.g. extensively and intensively managed meadows differ in the degree of management frequency.

The proportion of suitable habitat (fringes, mesoxerophytic and extensively managed grasslands) in a radius of 25 m around the experimental plots influences occurrence probability of butterflies. This circle covers an area twice as large as the experimental plot size of 30 m x 30 m, but within the natural size of fringes and mesoxerophytic grasslands in the nature reserve 'Hohe Wann'. This might stem from the fact that based on their high mobility habitat selection of butterflies takes place at a larger scale than the experimental plot size. On the other hand, the 'type of biotope' at our experimental plot should be highly correlated with the surrounding in 25 m, so that we could trace our result back to a technical reason. 'Type of biotope' represents a categorial variable in contrast to the metric variable 'suitable habitat in r = 25 m', which results in a decrease in degrees of freedom and thus increased model performance. This fact may also contribute to the exclusion of the 'type of biotope' and inclusion of the proportion of 'suitable habitat' in radii of 50 and 75 m in the model of *M. bicolor* respectively *P. albopunctata* as well. We can not easily differentiate between a technical failure or a real influence of the surrounding. Nevertheless, the composition of nearby habitats in the surrounding landscape will also affect the suitability of local habitat patches and thus population viability. For example, insects may utilise multiple habitat types during their life cycle (Noss 1990, Dunning et al. 1992, Villard et al. 1999, Sönderström & Pärt 2000) or they need to disperse between habitat patches. This depends on the quality of habitats in the surrounding landscape as well (Roland et al. 2000).

Test of transferability

Models based on the incidence of *C. arcania* can not be applied to other species. Additionally, the incidence of *C. arcania* can only be badly predicted by other species' occurrences. This may be due to the comparatively euryoceous properties of *C. arcania*. *C. arcania* is mesophilic, e.g. its habitats cover a broad range of types of biotopes. Habitats suitable for *Z. carniolica* and the investigated grasshopper and bush cricket species only cover a small part of habitat suitable for *C. arcania*. Vice versa only a small number of *C. arcania* habitats are suitable for the other species.

Occurrence probabilities of all five species studied can be best predicted with the model of the moth *Z. carniolica*. This species may thus act as representative or 'umbrella species' for others. However, this needs further investigations. In the models the variable 'type of biotope', vegetation height and the occurrence of the sucking plants *C. jacea* and *S. columbaria* play an important role. Thereby the two plant species may not directly influence grasshoppers and bush crickets but maybe they are indicators for extensively managed areas, which are preferred by the species.

Generally, stenoecious but mobile species may be best suited as 'umbrella' species (New 1995). They exactly represent habitat requirements of species typically found in specific habitats and can reach all potential habitats better than species with low mobility. Although one would expect that based on their higher mobility the moth *Z. carniolica* is much better suited as representative species for xerothermophilic species living on semi arid grasslands, in our case the transferability of the model of the moth *Z. carniolica* did only differ slightly (in one more successful transfer) from the one of the grasshopper *S. lineatus*. This may be due to the fact that mobility is not a decisive factor for the survival of this species in the nature reserve 'Hohe Wann', as connectivity is probably very high for *S. lineatus*. To really quantify this argument a landscape wide mapping of *S. lineatus* for the determination of connectivity would be necessary. Alternatively, one could test and compare the predictive quality of both models in other landscapes.

In general, the parameter 'type of biotope' showed a high potential for the prediction of species occurrence. Particularly, the models of the grasshopper *S. lineatus*, the bush cricket *M. bicolor* as well as the moth *Z. carniolica* can predict occurrence of the other species very well. This result may be of outstanding practical value, particularly in conservation biology, as the 'type of biotope' can be relatively easy determined in contrast to costly analyses of disturbance or vegetation structure and composition. Additionally, information on the type of biotope already exists for many regions of conservational interest. The type of biotope seems to reflect an aggregation of different parameters ranging from geological prerequisites (i.e. soils, slope) to anthropogenic influences (disturbance). Most importantly, it obviously also represents the perception of the environment by insect species. With reference to the MOSAIK project a prediction of the kind of type of biotope resulting from different management regime, e.g. by botanical analyses (Fritsch et al. in prep., Kühner & Kleyer in prep.), would allow for a classification of suitable and unsuitable areas for threatened species according to the type of management.

Chapter IV

Connectivity compensates for low habitat quality and small patch size in the butterfly *Cupido minimus*

Birgit Binzenhöfer, Robert Biedermann, Josef Settele and Boris Schröder

IN PREP. FOR ECOGRAPHY

Abstract
Habitat size, isolation and habitat quality are regarded as the main determinants of butterfly occurrence in fragmented landscapes. To analyse the relationship between the butterfly *Cupido minimus* and these factors, patch occupancy of the immature stages in patches of its host plant *Anthyllis vulneraria* was studied in the nature reserve Hohe Wann in Bavaria (Germany). 82 *A. vulneraria* patches were surveyed for presence of *C. minimus* in 2001 and 2002.

The occurrence was largely affected by the size of the food plant patches. In a habitat model using multiple logistic regression, management method and habitat connectivity were further determinants of species distribution. Internal and temporal validation demonstrates the stability and robustness of the developed habitat models. Additionally, it was proved that the colonisation rate of *C. minimus* was significantly influenced by the distance to the next occupied *Anthyllis* patch.

For long-term survival of (meta-)populations in fragmented landscapes the results show that lower habitat quality is compensated by higher connectivity between the host plant patches.

INTRODUCTION

In metapopulation biology habitat size and isolation are assumed to be the most important factors for the occurrence and long time survival of butterflies in fragmented habitats (Hanski & Gilpin 1991, Thomas et al. 1992, Hanski 1994a). Theoretical (Hanski 1994a, Hanski & Thomas 1994) and empirical studies (Harrison 1991, Hanski et al. 1994, Hill et al. 1996) among Lepidoptera have demonstrated, that the greater the patch size and the connectivity to other occupied patches, the higher the colonization probability. Contrary, extinction rates of local populations are higher in small and isolated patches. However, recent studies have demonstrated that habitat quality might be as well a good determinant of lepidopterans occurrence and improved the comprehension of metapopulation dynamics (Kuussaari et al. 1996, Dennis & Eales 1997, Thomas et al. 2001, Wahlberg et al. 2002). For example, Dennis & Eales (1997) asserted, that patch occupancy of *Coenonympha tullia* was as successfully explained by habitat quality as by habitat size and isolation together. And in the study of Thomas et al. (2001) habitat quality was the best predictor for the occurrence of three butterfly species in comparison to isolation and patch size. Thomas et al. (1998) showed within the genus *Maculinea*, that increasing extinction rates due to habitat loss and isolation could be much reduced - a minimum area preconditioned - if habitat quality will be optimised. According to Thomas et al. (2001) variation in habitat quality is the missing third parameter in metapopulation dynamics beside the conventional spatial parameters of isolation and area.

The aim of this study was to test which of the three factors better explains species distribution and to what extent they are responsible for species persistence. The study species, the Small Blue *Cupido minimus* (Fuessli, 1775) (Lepidoptera: Lycaenidae), is widely distributed in Europe but has declined strongly in many countries during the last decades (Asher et al. 2001). Therefore the results may enhance our understanding of the (meta-) population biology of *C. minimus* and help choosing effective conservation strategies.

Habitat models are widely used to specify functional relationships between species occurrence and its environment (Guisan & Zimmermann 2000, Austin 2002) and to quantify habitat requirements (Morrison et al. 1998). In this study we developed habitat models based on presence-absence data using logistic regression (Trexler & Trevis 1993, Guisan & Zimmermann 2000). Further, we analysed, whether colonisation and extinction were affected by the spatial configuration of the patches. To estimate the predictive performance of habitat models they should been transferred to independent data (Manel et al. 1999b, Schröder & Richter 1999, Guisan & Zimmermann 2000, Pearce & Ferrier 2000a, b, Reineking & Schröder 2003, Schröder & Reineking 2004). Beside internal validation techniques, we tested our habitat models also under different landscape conditions by externally validating the models in space and time.

MATERIAL AND METHODS

Study species

The Small Blue *Cupido minimus* colonizes poor, arid and often calcareous grasslands with Kidney Vetch (*Anthyllis vulneraria*) stocks (Ebert & Rennwald 1991, Weidemann 1995). The larvae feed only on *Anthyllis vulneraria* in the study area. *C. minimus* is a xerothermophilic species (Blab & Kudrna 1982) and is univoltine. The flight period in the study area lasts from the beginning of May until the beginning of July.

Cupido minimus occurs in Europe from Spain to Scandinavia, and also across Asia and Mongolia. While the distribution is assumed to be stable in many European countries, there is a serious decline especially in north–western Europe (up to 50% and more decrease in distribution in 25 years, Asher et al. 2001: 145-146). In Germany, Weidemann (1995) described the decline of this species for many regions in the last decades and *C. minimus* is regarded as „near threatened“ (Pretscher 1998). Agricultural intensification as well as abandonment are regarded as the main causes for the decline (e.g. Kudrna 1986, Feldmann et al. 1999).

Field work and identification of relevant habitat factors

The main study area, about 21 km², is the nature reserve „Hohe Wann“ in Northern-Bavaria, Germany (50°03' N, 10°35' E). The mean annual temperature is 8.8 °C and the mean annual precipitation 650 mm (Deutscher Wetterdienst 2002). The region is highly structured through the geological (Trias: Middle Keuper), geomorphological and microclimatic heterogeneity of the landscape. While the leveled areas (plateaus, valleys) are in intensive agricultural use, the slopes are more extensively used or are fallows. Thus, on the one hand, the landscape is characterised by a small-scaled mosaic of crop fields, fallow land and intensively managed meadows and on the other hand by poor grassland, thermophilic fringes, hedges and forests.

As the recording of *C. minimus* is most reliable by searching for the eggs and larvae at the flowerheads of *A. vulneraria* (Hermann 1999), in 2000 all patches of Kidney Vetch (n = 82) were mapped in the study area, using aerial photographs (scale 1:3500). *Anthyllis* patches were considered as separate, if they were at least 10 m apart. The size of small patches was measured in the field, for larger patches a Geographic Information System (GIS, ESRI ™ ArcView 3.2) was used. During the main flight periods in 2001 and 2002 the incidence of the immature stages of *C. minimus* was recorded in all *Anthyllis* patches. If the species was not detected at the first sampling occasion, the patch was searched for a second time at the end of the flight period. Each patch was scanned for eggs and larvae in time periods proportional to its area, with a maximum of 15 minutes per patch. The patch sizes range from 1 to 6300 m². Additionally further habitat parameters of the *Anthyllis* patches were recorded in the field: vegetation structure (e.g. plant cover, vegetation height) of the different vegetation strata and of the *Anthyllis*-plants, succession parameters (degree of bush encroachment) and the management regime (four different categories). "Insolation" parameters are exposition, inclination and scale of shading. The type of biotope (three different categories) was detected from a vegetation map in GIS (see Table 11 for more details). The complete survey of the *Anthyllis*-sites in the main study area enabled us to calculate patch isolation and connectivity. The distance to the next occupied *Anthyllis*-patch was used as a simple measure of isolation. Moreover, the connectivity S_i according to Hanski (Hanski 1994b, Moilanen & Nieminen 2002) was calculated using GIS:

$$S_i = \sum_{j \neq i} p_j \cdot \exp(-\alpha \cdot d_{ij}) \cdot A_j^{\ b} \qquad (2)$$

S_i = patch connectivity
p_j = occupancy of patch i [0 or 1]
α = parameter scaling the effect of distance on dispersal success
d_{ij} = distance between patch i and j measured from centre to centre [km]
A_j = size of patch j [m²]
b = scaling of immigration

Table 11: Habitat parameters of the *Anthyllis vulneraria* patches.

parameter	**unit / categories**
Anthyllis patch size	[m^2]
cover of *Anthyllis*	cover [%]
height of *Anthyllis*	[m]
type of biotope	extensively managed meadow / mesoxerophytic grassland / thermophilic fringes
type of management	mown grassland / cattle grazed meadows / sheepherding / fallow land
date of first management	until 15th June / until 15th July / until 15th August / after 15th August / fallow
inclination	[°]
sine exposition	[1]
cosine exposition	[1]
scale of shading	unshaded / partly shaded / largely shaded
cover of bush encroachment	cover [%]
height of bush encroachment	[m]
cover of shrub layer	cover [%]
height of shrub layer	[m]
cover of lower herb layer	cover [%]
height of lower herb layer	[m]
cover of upper herb layer	cover [%]
height of upper herb layer	[%]
cover of moss layer	cover [%]
cover of bare ground	cover [%]
connectivity S	scale of connectivity after Hanski
distance to the next occupied patch	[m]

Based on the results of Leon-Cortes et al. (2003) and Krauss et al. (2004) on *C. minimus* in Britain and Germany (Lower Saxony), respectively, as well as on the result of a colonisation experiment with two artificial *Anthyllis* patches in the main study area (unpubl. data) an average dispersal rate of 200 m was estimated. Consequently, we used $\alpha = 5$ and according to Krauss et al. (2004) $b = 1$, assuming a proportional rise of emigration rate with increasing patch area.

To test the transferability of the habitat models under different geographical conditions (Dennis & Eales 1998, Schröder & Richter 1999, Schröder 2000, Fleishman et al. 2003) an additional study area with *C. minimus* occurrence was chosen in 2002: the nature reserve Leutratal near Jena in Thuringia (50°52' N, 11°34' E). This study area (0.5 km^2) is characterised by shell-limestone slopes (lower Triassic limestones) of the river Saale valley covered with mesoxerophytic grassland at different successional stages (Heinrich et al. 1998, Hirsch et al. 1998). Normally, the grassland is mown in late summer (not before the end of July) or autumn. The climate is warmer (mean annual temperature is 9.3° C) and dryer (mean annual precipitation 587 mm) compared to our main study are in Northern-Bavaria (Heinrich et al. 1998).

Using an identical sampling protocol as in the main study area, 39 *Anthyllis* patches were found here with patch sizes ranging from 1 to 1500 m^2.

Statistical analyses

The relationships between the occurrence of *C. minimus* and the parameters area, connectivity (resp. isolation) and habitat quality of the patches were analysed using logistic regression. All statistical analyses were performed in SPSS ^{TM} (version 11.0).

Parameter selection

First, univariate analyses were conducted in order to find out the importance and relevance of each explanatory variable (Hosmer & Lemeshow 2000) before entering these parameters into a multiple model. Parameters with p-values > 0.2 were excluded from the analysis (Hosmer & Lemeshow 2000). The influence of the remaining variables was quantified by their odds ratios, a measure to estimate the effect of a predictor by specifying the ratio of odds between the presence or absence of a species when the value of the explanatory variable is altered by one unit. Further, the number of habitat parameters was reduced to avoid strong multicollinearity between the predictor variables. If there was a strong correlation between two explanatory variables (Spearman rank correlation $r_s > 0.5$, see also Fielding & Haworth 1995, Binzenhöfer et al. in prep. b, Strauß et al. in prep.) only the parameter correlated most strongly with the incidence was selected for further modelling. For multiple analyses the stepwise backward selection was used (Hosmer & Lemeshow 2000), with a significance level of $p_{in} = 0.05$ for the inclusion of a variable into the model and $p_{out} = 0.10$ for the exclusion of a variable (Schröder 2000).

Model evaluation

Different kinds of performance criteria can be used to evaluate a habitat model. Nagelkerke's R^2 quantifies the proportion of variance explained by the model. Values exceeding 0.4 indicate a good calibration (Backhaus et al 2000, Nagelkerke 1991, Steyerberg et al. 2001). Model discrimination describes the ability to correctly separate occupied from unoccupied habitats. Due to the failure to use all information of the classifier (Fielding & Bell 1997), a threshold independent measure for discrimination was applied: the area under the receiver operating characteristic curve (AUC). AUC-values above 0.7 describe an acceptable discrimination, values between 0.8 and 0.9 indicate a good and values above 0.9 an excellent discrimination (Hosmer & Lemeshow 2000). For the comparison of different alternative models we used the Akaike Information Criterion (AIC). The model with the lowest AIC represents the best compromise between goodness of fit and the lowest number of predictors (Buckland et al. 1997, Augustin et al. 2001).

Model validation

To test the accuracy and transferability of the habitat models, we applied different kinds of validation methods. Thereby the data set was splitted, one part was used for calibrating and the other for evaluating the model (Guisan & Zimmermann 2000, Schröder 2000). In this way it can be avoided that the model performance tends to be over-optimistic (Verbyla & Litvaitis 1989, Reineking & Schröder 2003). To judge the quality of the model predictions, independent, external data were used. We collected data in a second year in the main study area and in a second study area. Following Schröder (2000) we applied the significance test after Beck & Shultz (1986) to verify the transferability in space and time, whereby the evaluation is successfully, if the AUC-values of the model transfers significantly exceed a critical AUC-value (here: 0.7; cf. Bonn & Schröder 2001).

Effects of geographical parameters on population dynamics

Based on the two-year survey of the immature stages of *C. minimus,* the influence of geographical parameters on extinction rate and colonization rate was tested. The effects were analysed by logistic regression, with colonization event or extinction event, respecitvely, as dependent variable and area size, connectivity and distance to the next occupied *Anthyllis* patch as predictors.

RESULTS

Prevalence and spatial patch characteristics

In the nature reserve Hohe Wann the prevalence of the pre-imago stages of *C. minimus* increased from 55% in 2001 to 82% in 2002 (see Table 12), whereas the number of the *Anthyllis* patches decreased in the same period about 21% (2001: n = 82, 2002: n = 65). Eleven (2001) respectively four (2002) *Anthyllis* patches were found with only one or two plants. In both years three of them were occupied with eggs or larvae from *C. minimus*. Their locations were distant less than 100 m (2001: 11-73 m, 2002: 62-78 m). We detected the species in each of the thirteen patches larger than 1000 m^2. The mean distance to the next occupied *Anthyllis patch* was 182 m in 2001 and 203 m in 2002, respectively. In 2001 and 2002 the most isolated habitat was 1025 m away from the next *C. minimus* population with sizes of 500 m^2 and 588 m^2, respectively.

In the study area Leutratal all 39 patches were occupied by eggs or larvae in 2002. The distance of the patches ranges from 20 m to 115 m. The two largest *Anthyllis* patches measured 1500 m^2, the smallest 1m^2.

Table 12: Occupancy and spatial characteristics of the *Anthyllis vulneraria* patches.

	Hohe Wann 2001		**Hohe Wann 2002**		**Leutratal 2002**	
number of patches	82		65		39	
occupied patches [%]	45	(55%)	53	(82%)	39	(100%)
empty patches [%]	37	(45%)	12	(19%)	-	-
mean patch size [m^2] [min. / max.]	643	[1 / 6300]	792	[1 / 6300]	299	[1 / 1500]
mean patch size of occupied patches [m^2] [min. / max.]	1118	[1 / 6300]	936	[1 / 6300]	299	[1 / 1500]
mean distance [m] to the next occupied patch [min. / max.]	182	[11 / 1025]	203	[11 / 1025]	42	[20 / 115]

Effects of environmental factors on the occurrence of *C. minimus*

Selection and relevance of single parameters

After parameter reduction on the basis of univariate regression analyses and Spearman rank correlations only six variables remained for further modelling (see Table 13 for significance levels, R^2_N and odds ratios). Patch size yielded the highest explanatory power ($R^2_N = 0.39$). Per 100 m^2 area of larval food plants the odds ratio of *C. minimus* nearly doubled. Management regime had also a great influence on species occurrence. The most adequately managed sites are with extensive sheepherding followed by mown grasslands, cattle grazed meadows and fallow land. The parameter "date of first management" showed an unimodal response (Figure 6), whereas the period between middle of July and middle of August results in the highest predicted probabilities. Very early farmed sites (until 15th June) and particularly fallow land featured the lowest predicted probabilities. Within the parameter habitat type the odds ratio was sixfold at the extensively managed grassland and doubled at mesoxerophytic meadow in comparison to thermophilic fringes. Connectivity had a positive effect on the occurrence of *C. minimus*. Cover of shrub layer showed a negative, but slight influence on occurrence.

Table 13: Results of univariate logistic regression models, significance (p-value), R^2_N and odds ratios of the significant habitat parameters.

variable	p	R^2_N	categories	odds ratio (e^{β})
Anthyllis patch size	< 0.001	0.39		1.8 (per 100 m²)
type of management	0.004	0.20	fallow land	reference category
			mown grasslands	6.8
			sheepherding	31.5
			cattle grazed meadows	1.1
first time of management (inclusive squared term)	0.014	0.13	until 15th June / until 15th July / until 15th August / after 15th August / fallow	20.0 / 0.6 (per month)
type of biotope	0.010	0.14	thermophilic fringes	reference category
			extensively managed meadows	6.4
			mesoxerophytic grasslands	2.4
connectivity (α=5, b=1)	0.005	0.12	scale of connectivity after Hanski	11.4
shrub layer cover	0.194	0.03		0.3 (per 10%)

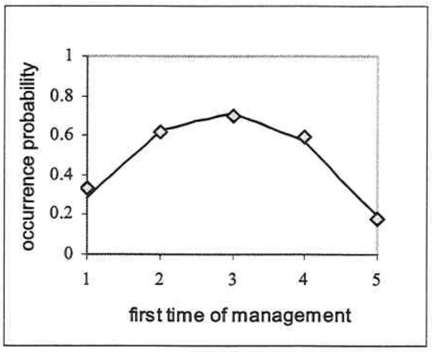

Figure 6: Response curve of a univariate model for the parameter time of first management. Predictor values at x-axis: 1 = until 15th June / 2 = until 15th July / 3 = until 15th August / 4 = after 15th August / 5 = fallow.

Multiple habitat models

As habitat suitability is mostly not specified by one parameter alone, a multiple logistic regression was performed to investigate the influence of different combinations of predictors on *C. minimus* occurrence.

Logistic regression with backward selection resulted in two significant models (Table 14). The parameter *Anthyllis* patch size and type of management were chosen in model I. The performance criteria indicate a good calibration and discrimination of the model after crossvalidation. Considering the variable connectivity and eliminating the type of management (model II) model performance was improved. The AIC value of model II is lower and the model discrimination is very good. In addition to patch size connectivity significantly influence *C. minimus* occurrence (see also Figure 7).

Table 14: Crossvalidated performance criteria of the multiple habitat models.

model	model parameter	R^2_N	AUC
I	*Anthyllis* patch size, type of management (AIC: 88)	0.48	0.76 [0.65 | 0.86]
II	*Anthyllis* patch size, connectivity (AIC: 85)	0.52	0.82 [0.73 | 0.91]

Patches exceeding sizes of 10 m² (log-value 1.0) enhance the predicted probability independently of habitat connectivity. At sites greater than 800 m² (log-value 2.9) the occurrence probability constitute 100%. For the highest connectivity value in the main study area (1.04) an occurrence probability of 80% is already predicted at very small sites (1 m²).

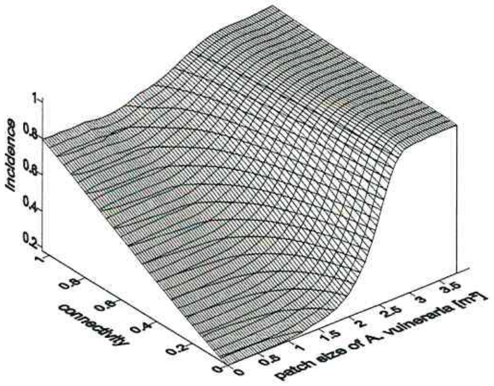

Figure 7: Response curve corresponding to the habitat model of the premature stages: response variable: predicted probabilities (z-axis), predictors: patch size ($\log_{10}$ transformed) and connectivity.

Therefore and as already demonstrated in the univariate models, the factor patch size plays the most important role for explaining *C. minimus* occurrence. In both multiple models the variance is mainly explained by patch size. Including the variable type of management in model I R^2_N increase from 0.39 to 0.48 and the AUC-value from 0.79 to 0.84. In the model II, which additionally contains the parameter connectivity, the R^2_N-value constitute 0.49 and the AUC-value 0.85 (Table 14).

Transferability of model results

The generality of the habitat models was tested by transferring them in time. The transferability in time (from 2001 to 2002) of both habitat models was significant (I: $p< 0.01$, II: $p < 0.001$; $AUC_{crit} = 0.7$). Validation by spatial model transfer was not possible, since *C. minimus* was recorded in all *Anthyllis* patches in the Leutratal.

Effects of spatial landscape structure on population dynamic processes

The total extinction rate of *C. minimus* from 2001 to 2002 was 10% (8 extinction events), whereof 6 patches went extinct due to patch eradication and 2 local *C. minimus* populations went extinct in persistent patches. The abandoned *Anthyllis* sites were 263 m and 1025 m from the next occupied patch and 64 m² and 500 m² in size. Due to the small sampling size (only two "real" extinction events) statistical analysis was not feasible.

All in all 16 (25%) of the persistent patches were (re)colonized for the first time in 2002. Within univariate logistic regression the distance to the next occupied patch was found to affect colonisation ($p < 0.04$, $R^2_N = 0.21$). The most distant patch, which was newly colonised, was 534 m apart from the next occupied patch and 180 m² in size. Though the influence of patch size on colonisation rate was positive, it was not significant ($p < 0.09$, $R^2_N = 0.14$). No relationship was found between colonisation and connectivity ($p < 0.76$, $R^2_N = 0.005$).

DISCUSSION

Effect of single environmental factors on habitat suitability for *C. minimus*

The influence of habitat quality factors

The target species was restricted to three biotope types: extensively managed meadows, mesoxerophytic grasslands, and thermophilic fringes. In contrast to Ebert & Rennwald (1991) *C. minimus* was predominantly recorded in extensively managed meadows and not in mesoxerophytic grasslands. This may be explained by the fact that many *Anthyllis* plants in the study area grew at locations which were cleared from bushes no more than a few years ago. Therefore many patches are currently just in a transitional stage between extensively managed meadows and mesoxerophytic grasslands, because a higher number and cover of typical species of mesoxerophytic grassland still have to immigrate at first, contrary to *Anthyllis vulneraria*, which is a pioneer on immature soils. Thermophilic fringes are the habitat type with the lowest prevalence in the nature reserve Hohe Wann. This effect could be traced back again to the fact that the cover of bush encroachment due to the extensive management is normally very high in fringes and this biotope type therefore is suboptimal for the larval food plant and probably for the xerothermophilic butterfly, too. The weak, but negative relationship between cover of shrub layer and *C. minimus* occurrence in the present study also forebodes this effect. Further, population size of *C. minimus is* negatively correlated with cover of shrub layer as demonstrated by Krauss et al. (2004) in a study near Göttingen in southern Lower Saxony (Germany). These results correspond with Ebert & Rennwald (1991) and Weidemann (1995), who regard early or initial successional stages as habitats for *C. minimus*.

"Date of first management" also influenced the occurrence of *C. minimus*. The highest predicted probabilities were found at sites managed between middle of July and middle of August after the majority of the larvae hatched out already. Very early farmed sites (until 15th June) and fallow land are most inappropriate, because the former as a rule have fertile soils and will be managed several times a year. Thus the immature stages of *C. minimus* will be damaged on the larval food plant. Furthermore, as pioneers are weak competitors, *Anthyllis vulneraria* will be swamped out. The latter locations will be unsuitable as a result of strong bush encroachment (see above).

In addition "type of management" explains species occurrence. *C. minimus* most strongly benefited from extensive sheepherding. Conspicuously less suitable were mown grasslands, followed by cattle grazed meadows. In agreement with management time the lowest occurrence probabilities were found on fallow grounds. To sum up, pasturing, if possible under avoidance of the development-phase of the immature stages, seems to be the most adequate management method for *C. minimus*, if management does not occur too frequently or too intensively (e.g. with cattle). On the one hand there still remain sufficient flowering *Anthyllis* plants for egg deposition or nectare, on the other hand bare ground will be generated, which again promotes this pioneer plant. Consequently, abandoned farmland negatively affects *C. minimus* occurrence. The study results correspond greatly with recommendations from other authors. According to Feldmann et al. (2000) *C. minimus* habitats should not be mown or intensively grazed before beginning of July. And also after Ebert & Rennwald (1991) overgrazing and wrong time-phased (at the development-phase of the immature stages) or repeated mowing per year should be avoided. Asher et al. (2001) advocated an adopted, extensive grazing regime in summer time resp. recommended pasturing in autumn or winter. From their point of view periodic ground disturbance may be essential on sites that cannot be grazed, as seeds of *Anthyllis vulneraria* can only germinate on bare ground. Ebert & Rennwald (1991) as well as Weidemann (1995) also highlight the potential importance of sites without natural cover for *Anthyllis* settlement and for *C. minimus* survival (like slopes with sparse vegetation or rural roads). Likewise, in the present study area such locations are occupied by *C. minimus*.

The influence of habitat connectivity and patch size

Habitat connectivity is an important factor influencing the presence of *C. minimus*. This fact is indirectly affirmed by Asher et al. (2001). In their study, the extinction risk of *C. minimus* populations was strongly increased by isolation of small habitat patches. In our study, the (landscape) variable with the highest explanatory power was *Anthyllis* patch size, which is confirmed by the investigations of Krauss et al. (2004). The high importance of food plant availability due to the strong dependency of immature stages on the host-plants, might be the limiting factor for butterfly distribution (Thomas et al. 2001). According to Krauss et al. (2004) connectivity nevertheless did not play a significant role for population size of *C. minimus*. The authors found *Anthyllis* patches with edge-to-edge distances up to 4.4 km, which were occupied by the target species. Presumably connectivity plays an important role for the persistence of *C. minimus* populations, whensoever the conditions are suboptimal. While the present study mainly took place in Keuper with only a small proportion of lime, the study of Krauss et al. (2004) was performed at soils of shell-limestone with a high proportion of lime, where *Anthyllis vulneraria* has its main distribution (Oberdorfer 2001). Thus the density of food plant and of *C. minimus* adults is much higher in shell-limestone regions like in the second study area Leutratal. There, but also near Göttingen, all *Anthyllis* patches were occupied without exceptions. Furthermore, logistic regression analyses conducted by Leon-Cortes et al. (2003: 473) confirmed that *C. minimus* in North Wales „usually went extinct when host plants were at low densities". In a mark-release-recapture study of *C. minimus* in chalk grassland in southern Belgium Baguette et al. (2000) did not observe butterfly movements between habitat patches, which are more than 762 m apart, although within their study exchange could theoretically have been observed with distances between 1334 m and 2568 m. Maybe the management between the Belgium habitats is too intensive (mainly fertilized grassland) and consequently dispersal corridors are not available. In general, according to Dennis & Eales (1997) habitat quality and patch size may be more influential factors for butterfly occurrence than isolation. But in areas where site eradication and fragmentation has progressed further, isolation is likely to be a more prominent factor (Dennis & Eales 1998).

Multiple habitat models

Multiple regression analyses resulted in two habitat models including three significant habitat factors (see Table 14). Beside the two landscape parameters patch size and connectivity, management type was the only factor among all habitat quality predictors which remained in the multiple model. This can be explained by the fact, that this variable integrates most of the relevant habitat conditions. The preferred land use type, sheep herding, mostly occurs in the study area on poor grasslands (extensively managed meadows or mesoxerophytic grasslands) during an optimal timeframe and prevent a high cover of shrub layer. Obviously, the type of management is a surrogate for the real factors driving habitat quality of *C. minimus*.

In model I *Anthyllis* patch size and type of management determine patch occupancy of the study species. According to the performance criteria, the second model including patch size and connectivity was still slightly better. Model calibration and discrimination of both versions are evaluated as good to very good. However, in the multiple model of Krauss et al. (2004) only patch size remained as a predictor. This may be explained by the fact, that i) the habitat factors investigated did not consider the management methods and ii) the habitat conditions are probably optimal and hence isolation effect did not effect occurrence (see above). The relationship between incidence, area size and connectivity (resp. isolation) is also known for other butterflies (Thomas & Harrison 1992, Hanski 1994b, Hill et al. 1996, Thomas & Hanski 1997, Dennis & Eales 1998, Gutierrez et al. 2001, Thomas et al. 2001) and other species groups (small mammals: Adler & Wilson 1985, Walker et al. 2003, leafhoppers: Biedermann 2000, 2004, grasshoppers: Kuhn & Kleyer 1999b). Patch size affects species presence because the habitat size is correlated with population size and large populations will become extinct less frequently (Wilcox 1980, Hovestadt 1990, Poethke et al. 1996). Connectivity is important for patch occupancy, as the colonisation probability of an unoccupied patch decreases with increasing isolation (Hanski 1994b). According to Leon-Cortes et al. (2003) the number of eggs and larvae of *C. minimus* is significantly correlated with the number of inflorescences per *Anthyllis* plant and as a result with habitat quality. Thomas et al. (2001) have demonstrated that - besides isolation and patch size - habitat quality is a major determinant of species survival. The persistence of three different butterfly species was two to three times better explained by variations in habitat characteristics than by site isolation. According to these authors, the three factors operate at different hierarchical levels. While habitat quality contributes more to species persistence, patch area and isolation more strongly influence the recolonisation of empty habitats. For instance, patch occupancy and extinction of the butterfly *Speyreira nokomis apacheana* were best modeled by measures of habitat quality, rather than by patch size and isolation (Fleishman et al. 2002). In other insect groups habitat characteristics also determine occupancy in addition to patch size and isolation (Biedermann 2000, Kuhn & Kleyer 1999b, Schröder 2000, Jonsen et al. 2001).

If habitat quality is high, also small and isolated habitats are suitable for butterflies (Thomas et al. 2001). This is affirmed by the investigations of Krauss et al. (2004), which detect 100% patch occupancy of *C. minimus* in spite of great variances in patch size and isolation. In the main study area of the present survey the prevalence of this species constitute 55% and 82%, probably due to the comparatively unfavorable habitat conditions. In contrast, in the nature reserve Leutratal with optimal geological formation and soil type for host plant settlement, all potential habitats were occupied. This comparison supports in turn the statement of Thomas et al. (2001), that habitat quality is the third parameter affecting (meta)population dynamics.

Both habitat models show a good to very good transferability in time. In contrast, the high patch occupancy was the reason, why spatial validation did not work. However, especially this fact highlights the general validity of the present multiple habitat models. *A. vulneraria* grows on extensively managed shell-limestone slopes in such high densities, that the maximum distance to the next *Anthyllis* patch is only 115 m and thus lower than the assumed mean dispersal distance of 200 m. The ubiquity of *C. minimus* in the nature reserve Leutratal could therefore be ascribed to high habitat quality, large *Anthyllis* sites and high connectivity.

Population structure and population dynamics of *C. minimus*

The results of our two-year survey of *C. minimus* in the main study area indicate a metapopulation structure (Hanski & Gilpin 1991, Hanski & Gilpin 1997, Reich & Grimm 1996). The species occupies discrete host plant patches separated by non-habitat and showed turnover in its incidence. Furthermore, population dynamics are assumed to be asynchronous as indicated by simultaneously occurring local extinction and (re)colonisation events. In their study on *C. minimus* in southern Belgium Baguette et al. (2000) also classified the network of colonies as metapopulation. Only two of three habitat patches were colonised due to low dispersal ability and high habitat isolation.

In our study the patch occupancy of *C. minimus* increased about 25% from 2001 to 2002, although the host plant distribution decreased about 21%. Asher et al. (2001) also report large fluctuations of *C. minimus* populations from year to year, possibly in relation to flowering cycles in the host plant. Leon-Cortes et al. (2003) suggest, that food plant dynamics strongly affect *C. minimus* persistence. The high colonisation rate in spite of the host plant decline in our study presumably results from the management history, rather than from recording bias in the previous year. The newly emerging foodplant patches due to the clearing of bushes a few years ago, were colonised with a delay, since *A. vulneraria* have to be one to five years old before they flower (Sterck et al.1982). As a result of the newly emerged *Anthyllis* patches, the extinction events of *C. minimus* are low (3%) in comparison to colonisation events. This again supports the statement of Baguette et al. (2000) that conservation of this species implies the creation of more closely related suitable patches.

Contrary to the occurrence probability of *C. minimus*, no relationship was found between colonisation rate and connectivity. However, there is a significant correlation between colonisation rate and distance to the next occupied patch. This may be traced back to the fact, that both attributes integrate different time frames and operate at different levels of population dynamic processes. Colonisation is influenced by the regional process of immigration and occurs from one year to the next. On the other hand, patch occupancy is more affected by processes at the local level (like birth and death), or by events dating back some time ago (e.g. management history, climatic disasters).

Connectivity and the distance to occupied patches are crucial factors, which must be considered together with dispersal capabilities of a species in order to build up an adequate habitat network for the persistence of a persistent metapopulation (Baguette et al. 2000). In the main study area, the maximum distance of *C. minimus* colonies to the next one was 1025 m. Immigration into habitat patches was observed over several 100 m's distance (534 m maximum) from occupied patches. In mark-recapture studies in Great Britain some movements over 1 km were detected, and vagrants 17 km from known colonies were recorded (Asher et al. 2001). However, the great majority of *C. minimus* individuals in a population is very sedentary. In Southern Belgium, 91% of the marked individuals remained in the same habitat during the flight period (Baguette et al. 2000) and the adults of the mark-recapture experiment in the UK rarely moved more than 40 m (Asher et al. 2001).

MAIN CONCLUSIONS

Our study demonstrates that *Anthyllis* patch size has the strongest effect on the occurrence of *C. minimus*, also when sometimes very small food plant patches were occupied. A further important factor is habitat quality, especially management type. For long-term survival of (meta-)populations in fragmented landscapes the results show that lower habitat quality is compensated by higher connectivity between the host plant patches.

Chapter V

Zusammenfassung

Verringerung der Habitatqualität, Lebensraumverlust und -verinselung sind die wichtigsten Gründe für den Rückgang vieler Arten (Amler et al. 1999). Das regionale Überleben von Arten in fragmentierten Landschaften kann langfristig durch ein ausreichend dichtes Netzwerk geeigneter Habitate gewährleistet werden, das eine Wiederbesiedlung von lokal ausgestorbenen Populationen ermöglicht (Kuhn & Kleyer 1999b). Die vorliegende Untersuchung hatte zum Ziel, mittels statistischer Habitatmodelle den funktionalen Zusammenhang zwischen Artvorkommen und Habitatqualität sowie räumlicher Habitatkonfiguration herauszuarbeiten. Des weiteren sollte die Prognosefähigkeit der entwickelten Modelle zur Artverbreitung getestet werden.

Im Naturschutzgebiet „Hohe Wann“ in den Hassbergen (Bayern) wurde die Inzidenz der Falterimagines von *Zygaena carniolica* und *Coenonympha arcania* auf 139 Zufallsprobeflächen in den Jahren 2001 und 2002 aufgenommen. Mit Hilfe logistischer Regressionsgleichungen wurde die Abhängigkeit des Artvorkommens von verschiedenen Habitatparametern untersucht, wobei auch der Einfluss der umgebenden Landschaft auf die Patch-Besetzung analysiert wurde. Das Vorkommen von *Z. carniolica* wird maßgeblich durch die Anwesenheit nährstoffarmer Grünlandbiotope (Extensivwiesen, thermophile Säume und Halbtrockenrasen) in der unmittelbaren Nachbarschaft (v.a. in einem Radius von 25 m) und von den beiden Saugpflanzen *Centaurea jacea* und *Scabiosa columbaria* bestimmt. *C. arcania* präferiert großflächiges, mageres Grünland (d.h., vor allem Extensivwiesen und Halbtrockenrasen innerhalb eines Radius von mindestens 100 m), das kleinräumig reich strukturiert ist durch Hecken bzw. Gebüsche und Säume. Optimalerweise werden die Flächen nach Mitte Juli oder nur unregelmäßig gemäht bzw. beweidet.

Um Vorkommensprognosen für das gesamte Untersuchungsgebiet erstellen zu können, wurden auch Modelle nur auf der Basis von flächenhaft verfügbaren Habitatinformationen, den Biototypen, erstellt. Für beide Falterarten konnten Habitateignungskarten mit einer hohen Vorhersagegenauigkeit angefertigt werden.

Im Rahmen von Habitatkonnektivitätsanalysen nach Keitt et al. (1997) konnte kein Effekt von Habitatgröße, Konnektivität bzw. Isolation auf das Faltervorkommen der beiden Arten nachgewiesen werden. Dies wird auf die hohe Dichte von sehr gut geeigneten Lebensräumen im Untersuchungsgebiet zurückgeführt.
Interne und externe Validierung weisen auf die hohe Robustheit und die generelle Anwendbarkeit der entwickelten Habitatmodelle hin. Aufgrund ihrer Übertragbarkeit in Raum und Zeit besitzen sie eine hohe Relevanz innerhalb der Naturschutzbiologie.

Inwieweit die Modelle auch zur Vorkommensprognose von Arten anderer Tiergruppen (Feld- und Laubheuschrecken) bzw. der gleichen Tiergruppe herangezogen werden können, wurde ebenfalls getestet. Unter den von Hein et al. (Kap. III) entwickelten Habitatmodellen für drei verschiedene Heuschreckenarten erwies sich das Modell für die Feldheuschrecke *Stenobothrus lineatus* als das beste zur Prognose der anderen untersuchten Arten. Auf der Basis der Parameter Biotoptyp und Vegetationshöhe wurden Vorkommensprognosen für die beiden Laubheuschrecken *Metrioptera bicolor* und *Platycleis albopunctata* sowie für die Falter *Z. carniolica* und *C. arcania* erstellt. Dabei war von allen Arten die Inzidenz von *C. arcania* am schechtesten vorhersagbar. Gleichzeitig konnte das beste verfügbare Modell von *C. arcania* nicht auf die anderen Arten übertragen werden. Als Erklärung dafür werden die vergleichsweise euryöken Habitatansprüche dieser Art diskutiert. Die besten Prognosegüten bei den Übertragungen lieferte das Modell von *Z. carniolica*, in das der Anteil geeigneter Biotopflächen (Extensivwiesen, thermophile Säume, Halbtrockenrasen) und die Saugpflanzen *Centaurea jacea* und *Scabiosa columbaria* einfließen. Auch wenn die beiden Pflanzenarten nicht direkt die Präsenz der Heuschrecken zu beeinflussen vermögen, gelten sie jedoch möglicherweise als repräsentative Indikatoren für extensiv bewirtschaftete Flächen, die von diesen Arten bevorzugt werden.

Weiterhin wurden Habitatmodelle für die Präimaginalstadien des Bläulings *C. minimus* erstellt. Dazu wurde 2001 und 2002 die Inzidenz der Eier und Raupen dieser Art in allen potentiellen Lebensräumen des Untersuchungsgebietes (Patches mit der Raupenfutterpflanze *Anthyllis vulneraria*; n = 82) aufgenommen. Neben der Abhängigkeit von der Habitatqualität, wurde auch der Einfluss der Habitatgröße und Habitatkonnektivität nach Hanski auf diese Art untersucht. Es zeigte sich, dass das Vorkommen von *C. minimus* maßgeblich durch die Patch-Größe der Wirtspflanze bestimmt wird. Weitere Prädiktoren sind die Bewirtschaftungsmethoden auf den *Anthyllis*-Flächen und die Konnektivität der Habitate.

Interne und zeitliche Validierung weisen auf die Robustheit der entwickelten Modelle hin. Zudem konnte festgestellt werden, dass die Kolonisationsrate von *C. minimus* signifikant durch die Distanz zum nächsten besetzten *Anthyllis*-Patch beeinflusst wird. Die Ergebnisse zeigen, dass für das langfristige Überleben von (Meta-)Populationen in fragmentierten Landschaften eine geringe Habitatqualität durch eine hohe Konnektivität zwischen den Wirtspflanzenbeständen ausgeglichen werden kann.

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Curriculum vitae

Birgit Binzenhöfer
Friedhofstr. 1
97475 Zeil / Main

- geboren am 26. Mai 1969 in Limbach am Main / Bayern
- 1975 bis 1979: Grundschule Eltmann
- 1979 bis 1981: Hauptschule Eltmann
- 1981 bis 1988: E.T.A.-Hoffmann-Gymnasium Bamberg
- Januar bis Juni 1989: "Arbeiten und Lernen"-Maßnahme "Umwelt- und Naturschutz" des Verbandes der Volkshochschulen in Kooperation mit dem Landkreis Haßberge
- Juni bis August 1989: Büroaushilfskraft bei FAG Kugelfischer Eltmann
- Oktober 1989 bis April 1997: Studium der Diplom-Geographie, Fachrichtung Biogeographie, an der Universität des Saarlandes

  Diplomarbeit: "Vergleichende autökologische Untersuchungen an *Maculinea nausithous* und *Maculinea teleius* (Lepidoptera: Lycaenidae) im nördlichen Steigerwald"
- seit Mai 1997: Freiberufliche Tätigkeit im Bereich Arten- und Naturschutz, Landschaftsökologie und –planung
- August 1998 bis Mai 2000: angestellt im Fachbereich Landespflege beim Wasserwirtschaftsamt Schweinfurt
- seit Juni 2000: Doktorandin im „MOSAIK"-Projekt bei PD Dr. Josef Settele am Umweltforschungszentrum Leipzig-Halle

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UFZ-Umweltforschungszentrum
Leipzig-Halle GmbH
Permoserstraße 15, 04318 Leipzig
Internet: www.ufz.de