Ausbreitung und Etablierung der Europäischen Gottesanbeterin *Mantis religiosa* in Deutschland unter dem Einfluss des Klima- und Landschaftswandels

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Eine modifizierte Form des Kapitels 4 dieser Arbeit ist in Vorbereitung zur Veröffentlichung.

Orbital consequences

The sun and the earth describe orbital changes
   which drive climate cycles and modify ranges.
The shape of the land forms a number of places
   that allow the survival of different races.
When enclaves advance with the ice in retreat
   some form hybrid zones where two ranges meet.
Such regions are common and not very wide
   so the mixing of genes affects neither side.
They divide up the range in a patchwork of pieces
   with echoes and glimpses on the nature of species.
A brief rendez-vous and the ice comes again.

When the glaciers melt so that ranges expand
   some plants will spread quickly where there's suitable land.
Those insects which eat them will follow this lead
   some flying, some walking to establish their breed.
Those that try later meet a resident band,
   they must somehow be better to make their own stand.
But the mixture will change as more types arrive
   and warming conditions allow new species to thrive.
Some will move on to fresh places ahead,
   those that remain must adapt, or are dead.
And then the tide turns and the ice comes again.

Each refuge could foster a deviant form,
   new neighbours, chance changes and drift from the norm.
When the warm breakout comes, those few in the van
   disperse from the edge and breed where they can.
Pioneer pockets grow to large populations,
   a very good place to strike new variations.
Some may not work well with their parental kind
   so stopping the spread of those from behind.
Continental theatres provide plenty of chances
   to establish new morphs in both retreats and advances.
New species may form when the ice comes again

So what will you do when the ice comes again?
   It could be quite quick, if the ice cores speak plain.
The great ocean currents that warm our green spring
   may stop in a season should the salt balance swing.
Great civilizations in north temperate lands
   must migrate south to the sun and the sands.
But past pollen and dust tell us these will be drier,
   wet forests will shrink and population grow higher.
Our forebears hung on near a sea or a cave.
   They fished and they painted, they dreamed, they were brave.
So like Noah and Eric, we must adapt and survive.

G. M. Hewitt

Molecular Ecology 10:537-549

INHALTSVERZEICHNIS

1 ALLGEMEINE EINLEITUNG

1.1 Klimawandel und seine Auswirkungen

Seit einigen Jahrzehnten werden global klimatische Veränderungen beobachtet (IPCC 2014). Diese Veränderungen haben trotz einzelner lokaler Temperaturabnahmen weltweit eine Zunahme der durchschnittlichen Jahrestemperatur, Veränderungen in den Niederschlagsmengen und die Häufung von Extremwetter-Ereignissen (Katz & Brown 1992; IPCC 2014) zur Folge. Aufgrund der Temperatur- und Niederschlagsveränderungen trat in den letzten 50 Jahren in der nördlichen Hemisphäre eine Verfrühung saisonaler Ereignisse um 2,3 bis 5,1 Tagen pro Dekade ein (Thuiller 2007).

Klimatische Veränderungen haben einen großen Einfluss sowohl auf aquatische als auch auf terrestrische Ökosysteme (Stachowicz et al. 2002; Walther et al. 2002; Parmesan 2006; Vagg & Hepworth 2006; Burgmer et al. 2007; Thuiller 2007). So konnte in den letzten Jahrzehnten unter dem gegenwärtigen Klimawandel und der damit einhergehenden Verschiebung der Klimazonen (Dillon et al. 2010), weltweit eine Veränderung der Verbreitungsgrenze vieler Organismen beobachtet werden (Vitousek et al. 1996; Root et al. 2003; Parmesan 2006; Thuiller 2007). In der nördlichen Hemisphäre haben sich die Verbreitungsgrenzen von Pflanzen- und Tierarten pro Dekade im Schnitt um 6,1 km nordwärts oder in 6,1 m höher gelegene Regionen verschoben (Thuiller 2007). Auch in Europa verschieben sich die Verbreitungsgrenzen diverser Tier- und Pflanzenarten (Walther et al. 2002; Luterbacher et al. 2004; Wilson et al. 2005; Parmesan 2006; Walther et al. 2009; Robinet & Roques 2010). Für Großbritannien konnte eine Studie zu Tierarten verschiedener taxonomischer Klassen (Amphibien, Arachniden, Aves, Diplopoden, Insekten, Malacostraceen, Mammalia und Teleostei) eine Verschiebung der Verbreitungsgrenzen im Schnitt um 24,8 km nordwärts und 10,1 m in höhere Regionen pro Dekade zeigen (Hickling et al. 2006). Andere Studien zeigen auch für das europäische Festland eine Verschiebung der Verbreitungsgrenzen in nördliche Richtung beispielsweise für Falter- (Parmesan et al. 1999; Robinet et al. 2007; Sparks et al. 2007), Libellen- (Braune et al. 2008), Vogel- (Rupp & Saumer 1996) und Fischarten (Beare et al. 2004).

Das Vorkommen und damit einhergehend die Verschiebung der Verbreitungsgrenzen einer Art hängt unter anderem von ihrer phänotypischen und genotypischen Plastizität, und somit von ihrer Anpassungsfähigkeit an ihre Umwelt ab. Am Rand des Verbreitungsgebietes einer Art können die Umweltbedingungen so stark schwanken, dass sie außerhalb des Toleranzbereiches der Art liegen können und damit die Pionierpopulationen wieder aussterben. Da Arten nur in artspezifischen und stabilen Habitaten mit für sie guten bis optimalen Lebensbedingungen langfristig überleben und stabile Populationen bilden können (Pulliam 2000), bedingen Umweltschwankungen am Rande des Verbreitungsgebietes einer Art einen wiederkehrenden Prozess der Kolonisation und Extinktion (Walther et al. 2002). Infolgedessen sterben kaltangepasste Organismen bei der Zunahme der Temperatur in ihren ehemaligen Lebensräumen aus bzw. wandern ab und überleben in kühleren, meist nördlicheren oder höher gelegenen Regionen (Parmesan 2006; Thomas et al. 2006). Gleichzeitig eröffnen die Klimawandel-bedingten Temperaturzunahmen aber auch Lebensraum für neue Arten. So wird vermehrt beobachtet, wie warm angepasste Organismen aus dem südeuropäischen und mediterranen Raum neue für sie klimatisch geeignete Lebensräume in Zentraleuropa besiedeln (Sparks et al. 2007; Walther et al. 2009). Bei Insekten ist die Besiedlung stark temperaturabhängig, da Temperatur sowohl einen Einfluss auf ihre Entwicklung (Ingrisch 1978; Bale et al. 2002; Walters et al. 2006; Buse & Griebeler 2011) als auch auf ihre Bewegung (Taylor 1963) hat.

Neben geeigneten Habitaten spielt bei der Ausbreitung auch das Bewegungsvermögen und damit einhergehend die Ausbreitungsfähigkeit einer Art eine wesentliche Rolle (Brechtel 1996).

1.2 *Mantis religiosa* in Deutschland

Eine thermophile Insektenart, die sich in Europa unter dem Klimawandel in nördliche Richtung ausbreitet, ist die Gottesanbeterin *Mantis religiosa* (Detzel & Ehrmann 1998). Ihr Hauptverbreitungsgebiet in Europa liegt im mediterranen Raum sowie in Südost- und Osteuropa. Aktuell verläuft ihre nördliche Verbreitungsgrenze von Nordfrankreich über Westdeutschland, Norditalien bis nach Südpolen (Detzel & Ehrmann 1998; Liana 2007; Berg et al. 2011). Seit einigen Jahrzehnten scheint sich die Verbreitungsgrenze von *M. religiosa* in Deutschland von den südbadischen Vorkommen in nördliche Richtung entlang des Rheins zu verschieben (Brechtel 1996; Walther et al. 2009; Robinet & Roques 2010). Seit den 90iger Jahren existieren stabile Populationen im südlichen Rheinland-Pfalz und Saarland (Niehuis 1995). Auch im Norden und Osten Deutschlands leben mittlerweile erste *M. religiosa* Populationen (Berlin, Brandenburg, Sachsen und Sachsen-Anhalt, Berg et al. 2011; Ehrmann & Reinhardt 2011).

Die verstärkte Ausbreitung wird mit der Zunahme geeigneter Lebensräume in Verbindung gebracht. Die Entstehung solcher Lebensräume kann durch extreme Temperaturereignisse im Rahmen des Klimawandels begünstigt werden (Detzel & Ehrmann 1998; Schwarz-Waubke et al. 2002). Es wird angenommen, dass sich *M. religiosa* in Mitteleuropa, bedingt durch die prognostizierte klimatische Erwärmung, weiter nach Norden ausbreiten wird (Brechtel 1996; Detzel & Ehrmann 1998; Geiter et al. 2002; Cannings 2007; Liana 2007).

Ein Grund für das bisher räumlich limitierte Vorkommen von *M. religiosa* in Deutschland liegt in ihren Temperaturpräferenzen: *Mantis religiosa* ist eine xerothermophile, rein insektivore Art und ist in großen, arthropodenreichen Biotopen sehr standorttreu (Schwarz-Waubke et al. 2002). Sie hält sich vorzugsweise in offenen, trocken-warmen und sonnigen Gebieten auf, wie beispielsweise in den extensiv genutzten Weinbergen des Kaiserstuhls oder auf xerothermen, sonnigen Wiesen (Detzel & Ehrmann 1998). Auf solchen Flächen schlüpfen die Larven bei warmen Temperaturen Ende Mai/ Anfang Juni und benötigen für eine erfolgreiche Entwicklung bis zum Imago viel Nahrung und Wärme. Zwei Wochen nach der letzten Larvalhäutung (August/ September) sind die Fangschrecken geschlechtsreif und legen zwei bis drei Tage nach der Paarung ihre Eier in Eipaketen, sogenannten Ootheken, ab (Detzel & Ehrmann 1998). Im Gegensatz zu den Imagines, die im Spätherbst sterben, überwintert jenseits der nördlichen 10° Januarisotherme die Art im Eistadium bis zum nächsten Frühjahr, gut geschützt in ihren Ootheken (Beier 1968; Detzel & Ehrmann 1998; Stärz et al. 2010).

Ein weiterer Grund für das limitierte Vorkommen der *M. religiosa* ist ihr sedentäres Verhalten: Als Lauerjäger und aufgrund der generellen Flugträgheit wird *M. religiosa* bei ausreichendem Nahrungsangebot als sehr sesshaft und standorttreu eingeschätzt (Ehrmann 1985; Hevers & Liske 1991; Detzel & Ehrmann 1998). Der beobachtete individuelle Bewegungsradius während der gesamten Adultphase schwankt bei männlichen *M. religiosa* zwischen 10 m und 270 m (Hideg 1994; Liana 2007) und reicht bei weiblichen Fangschrecken von 0 m bis maximal 160 m (Hideg 1994; Stärz et al. 2010). Generell wird ihre Ausbreitung als eher passiv und zufällig beschrieben. Flugfähige Imagines können beispielsweise durch Wind verdriftet werden oder die Eigelege (Ootheken), die im Herbst an Zweige, Gräser und Steine geheftet wurden, werden durch Menschen oder Tiere verschleppt (Beier 1968; Niehuis & Schulte 1993; Brechtel et al. 1996; Schwarz-Waubke et al. 2002; Cannings 2007; Liana 2007).

Aufgrund dieser eingeschränkten Eigenschaften ist die verstärkte Ausbreitung von *M. religiosa* in den letzten Jahrzehnten erstaunlich. Es wird daher vermutet, dass die aktive Dispersionsfähigkeit von *M. religiosa* in Fachkreisen bisher unterschätzt wurde. Bereits Stärz et al. (2010) stellten fest, dass *M. religiosa*-Habitate, die im Winter gerodet wurden, also absolut frei von Individuen und Ootheken waren, innerhalb einer einzigen Entwicklungsperiode erneut wiederbesiedelt wurden.

1.3 Motivation und Ziel der Arbeit

Aufgrund ihrer Seltenheit und ihres eingeschränkten, gefährdeten Lebensraumes (Halbtrocken- und Trockenrasen, offene xerotherme Brachflächen; vergl. Pfeifer, Niehuis & Renker 2011), ist die Gottesanbeterin in Deutschland gesetzlich „besonders geschützt" (BArtSchVo, Fassung vom 29.07.2009). Der Landschaftswandel, die Fragmentierung der Landschaft, Pestizide und potentiell negative Einflüsse des Klimawandels auf *M. religiosa*, wie beispielsweise eine nicht auszuschließende Zunahme von Frühjahrsniederschlägen in Deutschland (Jacob 2008; Schönwiese 2008), die die Ei- und Larvenentwicklung dieser thermophilen Art stark einschränken (Brechtel et al. 1996; Berg et al. 2011), gefährden *M. religiosa* (Detzel & Ehrmann 1998; Berg et al. 2011). Um diese Art weiterhin angemessen in Deutschland zu schützen und eventuelle Schutzvorkehrungen zum Erhalt dieser Art und ihrer Lebensräume zu treffen, ist es wichtig ihre Herkunft, die Habitatbedingungen, die stabile Populationen ermöglichen und ihre Dispersionsfähigkeit zu kennen.

Das Ziel meiner Promotionsarbeit war die Ausbreitung und Etablierung von *M. religiosa* in Deutschland besser zu verstehen, um basierend auf diesem Wissen daraus später Schutzmaßnahmen für die Art formulieren zu können. Zudem können meine Ergebnisse modellhaft für die Beurteilung von Ausbreitungsprozessen thermophiler Insekten unter dem weiter fortschreitenden Klima- und Landschaftswandel genutzt werden.

Über die Herkunft von *M. religiosa* in Deutschland gab es in Fachkreisen bislang nur Vermutungen, über die jedoch Uneinigkeit herrschte. Da bisher noch keine aufschlussreiche Untersuchung zur Herkunft und Ausbreitung von *M. religiosa* in Deutschland vorlag, analysierte ich die Herkunft von deutschen *M. religiosa* Populationen mit genetischen Methoden (Kapitel 2). Zur Rekonstruktion ihrer bisherigen Ausbreitung untersuchte ich mithilfe von Sequenzanalysen von mitochondrialen Markern die Verwandtschaft deutscher *M. religiosa* Individuen mit *M. religiosa* Individuen aus Nachbarländern (Phylogeographie, Avise et al. 1987). Anhand meiner Daten konnte ich eine erste Aussage über die Ausbreitung von *M. religiosa* in Europa machen. Sie zeigen eindeutig, dass *M. religiosa* aus benachbarten Ländern nach Deutschland einwandert.

Erste Erkenntnisse zu benötigten Habitatbedingungen für das Überleben von *M. religiosa* Populationen in Deutschland geben Stärz et al. (2010). Neben der Auswirkung von winterlicher Brandrodung auf *M. religiosa* Populationen untersuchten diese Autoren die Aufenthaltsorte von *M. religiosa* in Bezug auf Umweltparameter, wie der Himmelsrichtung, Vegetationsstruktur, potentieller Sonnenscheindauer etc., ohne jedoch die mikroklimatischen Parameter Temperatur und relative Luftfeuchte im Einzelnen zu berücksichtigen. Da jedoch auch diese beiden Parameter für die erfolgreiche Entwicklung von Insekten und ihrer Etablierung in einem Gebiet ausschlaggebend sind (Franz 1931; Franz 1933; Röber 1949), analysierte ich das Vorkommen von *M. religiosa* in Bezug auf mikroklimatische Habitatbedingungen auf zwei Untersuchungsflächen. Hierfür untersuchte ich die Mikrohabitatpräferenz verschiedener Stadien von *M. religiosa* innerhalb ihres Lebenszyklus (Kapitel 3) indem ich Fang-Markierung-Wiederfang-Versuche mit Imagines im Freiland durchführte und das Vorkommen der einzelnen Lebenszyklus-Stadien auf den Flächen rasterbasiert erfasste. Zeitgleich erhob ich auf den beiden Untersuchungsflächen rasterbasiert abiotische und biotische Parameter, wie Habitatstrukturen, Vegetationshöhen, Temperatur und relative Luftfeuchte in verschiedenen Mikrohabitaten. Die Modellierungen der Fang-Markierung-Wiederfang-Ergebnisse zeigten deutliche Habitatpräferenzen von männlichen und weiblichen *M. religiosa*. Auch für die Wahl der Ootheken-Ablageplätze, für den Oothekenschlupf sowie tendenziell für die Imaginalhäutung konnte ich Präferenzen für Habitatstrukturen und für klimatische Bedingungen ausmachen.

Da im Untersuchungszeitraum Biotoppflegemaßnahmen auf beiden Untersuchungsflächen durchgeführt wurden, mache ich in Kapitel 3 zusätzlich eine Abschätzung zu den Auswirkungen der angewandten Mäh- und Beweidungsmethoden und führe entsprechende Verbesserungsvorschläge für die beiden untersuchten Populationen ein.

Neben den passenden Umweltbedingungen benötigen Arten für ihre Ausbreitung und den genetischen Austausch zwischen Populationen Habitate, die sich im Bewegungsradius der Individuen befinden. Bei hoher Abundanz oder ungeeigneten Umweltbedingungen können Individuen entsprechend auf Nachbarhabitate ausweichen, welches eine eventuelle Extinktion der ansässigen Population verhindern kann. Um solche Trittstein-Habitate im Rahmen von Schutzmaßnahmen zur Verfügung stellen zu können, muss die Dispersionsfähigkeit der Art bekannt sein. Bereits Stärz et al. (2010) und Liana (2007) haben das individuelle Bewegungsverhalten von *M. religiosa* untersucht, um den Individuenaustausch zwischen Habitaten abzuschätzen. Die Beobachtungen dieser Autoren beschreiben allgemein das Bewegungsverhalten der Individuen zwischen unterschiedlichen Flächen, ohne jedoch den Einfluss der vorherrschenden klimatischen Bedingungen zu beachten. Da neben der

Entwicklung auch die Bewegung und damit einhergehend die Ausbreitung von Insekten temperaturabhängig ist (Taylor 1963; Walters et al. 2006), untersuchte ich die Dispersion von *M. religiosa* unter dem Einfluss der vorherrschenden klimatischen Bedingungen, um so den Einfluss des Klimawandels auf ihre Ausbreitung besser abschätzen zu können (Kapitel 4). Für diese Untersuchung nutzte ich ebenfalls die Daten aus den Fang-Markierung-Wiederfang-Versuchen sowie die bereits für Kapitel 3 erhobenen klimatischen Daten der beiden Untersuchungsflächen. Zusätzlich ermittelte ich die zurückgelegten Distanzen von *M. religiosa* Individuen zwischen den Wiederfängen. Da *M. religiosa* als Lauerjäger sehr sedentär ist, untersuchte ich den Einfluss der klimatischen Parameter Temperatur und relative Luftfeuchte getrennt für die Bewegungswahrscheinlichkeit und die Bewegungsdistanz zwischen den Wiederfängen. Die Berechnungen zeigten erwartungsgemäß einen Effekt der klimatischen Parameter auf die Bewegung von *M. religiosa*. Als Lauerjäger zeigt *M. religiosa* jedoch im Vergleich zu anderen Insektenarten eine abweichende Reaktion auf steigende Temperaturen.

2 RECONSTRUCTION OF TWO COLONISATION PATHWAYS OF *MANTIS RELIGIOSA* (MANTODEA) IN GERMANY USING FOUR MITOCHONDRIAL MARKERS

2.1 Abstract

Past and recent climatic changes induced shifts in species ranges. *Mantis religiosa* has also expanded its range across Germany within the past decades.

To determine the ancestry of German *M. religiosa* we sequenced four mitochondrial genes (COI, COII, Cyt b, ND4) of European *M. religiosa* populations. We found an east, central and west European lineage of *M. religiosa*. These distinct lineages are consistent with genetic isolation by distance during glacial periods, and the re-colonization of northern parts of Europe by species from different refugia. Within Germany, we found haplotypes clustering to the central and west European lineage suggesting that *M. religiosa* immigrated from two directions into Germany. Mismatch distributions, and negative Tajima's D and Fu's Fs values indicate a current range expansion of the central and west European lineage. We hypothesise that ongoing global warming which increases the availability of thermally favourable areas in Germany for *M. religiosa* adds to its current range expansion.

In conclusion, *M. religiosa* colonized Germany via two directions: west German populations descended from French populations and east German populations from Czech populations.

2.2 Introduction

Past and recent climatic changes are causing geographic range shifts of species (Root et al. 2003; Parmesan 2006). Within Europe, as a consequence of recent ongoing global warming, numerous plant, bird and insect species have expanded poleward (Walther et al. 2002; Parmesan 2006; Robinet & Roques 2010). For instance, several insect taxa have shifted their range margin on average between 11 and 104 km northwards since 1960 (Hickling et al. 2006).

At the edge of a species distribution, colonisation and extinction are recurring processes: Pioneering individuals continuously disperse and create new populations. Only in species-specific, optimal, and stable habitats can species survive and reproduce (Pulliam 2000); in climatically unfavourable habitats, newly established populations become extinct within a short period of time.

As a consequence of global warming, also the praying mantis *Mantis religiosa* (LINNAEUS, 1758) has strongly expanded northward in Europe during the past decades (Brechtel 1996; Liana 2007; Robinet & Roques 2010). Its major geographic distribution in Europe covers southern Europe with Spain and Italy, the Balkan States in southeastern Europe and eastern Europe. The northern distribution border is currently found in France, western Germany and southern Poland (Fig. 2.1 (a); Detzel & Ehrmann 1998; Liana 2007; Berg et al. 2011). Sporadic records of *M. religiosa* in Germany exist since 1756 (Harz 1957). These indicate recurring immigration events of *M. religiosa* into Germany and the absence of suitable environmental conditions to establish stable populations over long periods. Since the second half of the nineteenth century stable populations exist in thermally favourable areas of southwestern Germany (Baden-Württemberg, summarised in Berg et al. 2011), and the number of records has steadily increased. Currently, *M. religiosa* populations exist in western and eastern Germany (Berg et al. 2011).

The origin of German *M. religiosa* populations has not been studied, yet. Some authors assume that *M. religiosa* is expanding from local German remnant populations established from previous immigration events (Harz 1957; Aspöck 2008). Other authors suppose a recent immigration of *M. religiosa* into Germany from adjacent countries (Detzel 1995; Detzel & Ehrmann 1998).

In order to resolve the ancestry of German *M. religiosa* populations, we examined its dispersal history by genetic analyses of mitochondrial genes.

Assuming that *M. religiosa* immigrated into Germany during the last decades and centuries, the exclusive clustering of *M. religiosa* populations in western and eastern Germany led us to presume two colonization directions: one from western Europe and one from central Europe (Fig. 2.1(b)). Such colonization directions both coincide with known postglacial expansion routes of various species (Hewitt 1999; Aspöck 2008). According to this hypothesis, we expected a close genetic similarity between west German and French populations and between east German and central European populations.

To reconstruct the ancestry of *M. religiosa* populations in Germany we analysed four mitochondrial genes of German *M. religiosa* populations and of putative source populations from six countries adjacent to Germany (Fig. 2.1(a), Table 2.1). The German *M. religiosa* populations were too small to sample a sufficient number of individuals for microsatellite analyses. Yet, mitochondrial markers have been successfully applied to study recent range expansions of species (Scataglini et al. 2006; Barr 2009; Zitari-Chatti et al. 2009; Hammouti et al. 2010; Li et al. 2011; Reis et al. 2011).

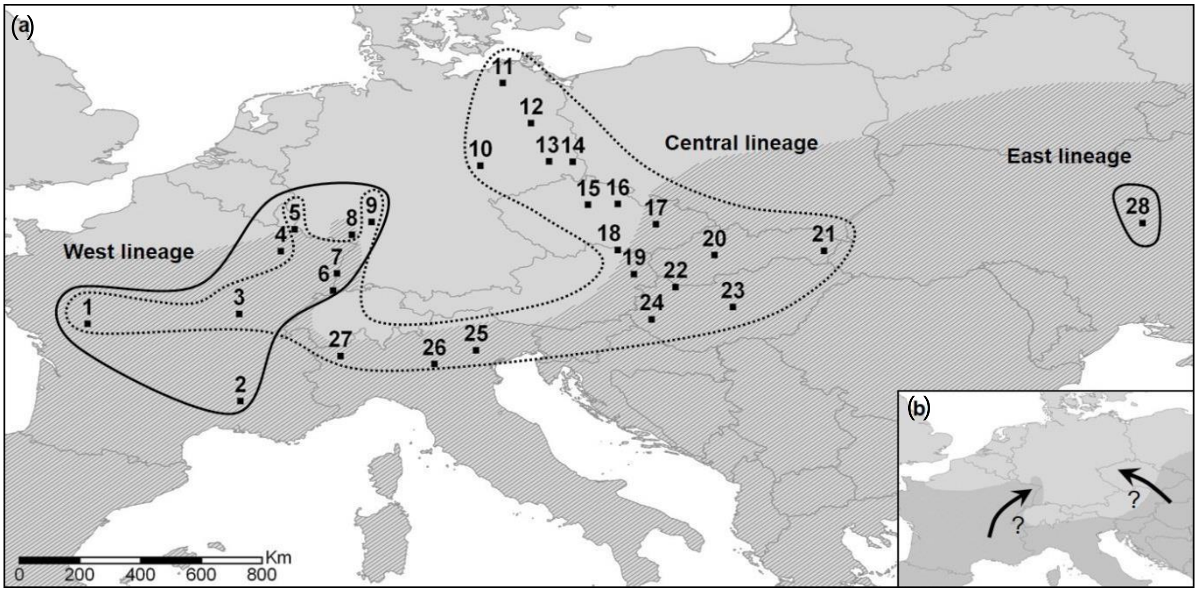

Fig. 2.1(a). Map showing sampled locations of *M. religiosa* in Europe. The range of *M. religiosa* is shaded (situation in 2010, after Berg et al. 2011). Numbers next to locations (squares) refer to location numbers (see Table 2.1). Major genetic lineages derived from SAMOVA (Dupanloup et al. 2002) and supported by further analyses are encircled (West, Central, and East lineage). West German populations descend from the West lineage and east German populations descend from the Central lineage. (b) Possible expansion routes of *M. religiosa* into Germany.

2.3 Material and Methods

2.3.1 Study species Mantis religiosa

The thermophilic insect species *M. religiosa* typically inhabits open and dry landscapes (Detzel & Ehrmann 1998; Liana 2007; Berg et al. 2011). As a territorial sit-and-wait predator it mainly feeds on arthropods (Harz 1957; Ehrmann 1985; Hideg 1994; Liana 2007; Berg et al. 2011) and has a low dispersion ability (Hideg 1994; Liana 2007). Hence, cold and wet springs and summer seasons are detrimental to the survival of *M. religiosa,* as such conditions reduce arthropod abundance (Brechtel 1996; Liana 2007).

2.3.2 Sampling design

We gathered tissue samples and DNA isolates of 171 *M. religiosa* individuals from locations across its current northern distribution in Europe to cover all putative geographic origins of German *M. religiosa* populations (Fig. 2.1(a), Table 2.1). We collected tissue samples (one tarsus) from wild individuals and from private and museum collections (Naturkundemuseum

Karlsruhe, SMNK). Tissue samples were stored in > 80% ethanol and kept either at 4°C or at room temperature. Additional DNA-isolates of individuals were kindly provided by P. Janšta (Charles University in Prague). DNA from tissue samples and from isolates was of high quality (except for 13 samples, Table 2.1).

Samples originated from 44 geographical locations and were collected from individuals between 2002 and 2012. We used individuals from the geographically distant Ukraine as the genetic outgroup.

Table 2.1. Sampled populations used in the genetic analysis to reconstruct the ancestry of *M. religiosa* in Germany. Individuals of locations separated by distances of less than 50 km are pooled under a single site number and treated as one population (for example individuals of locations Bollène, Pouzol, Ornac-l'Aven, Labastide-de-Virac and Sérignan-du-Comtat are pooled to site No. 2). Only for the outgroup Ukraine we pooled individuals from locations sampled within a wider range than 50 km to one site. In order to avoid misinterpretation, we did not calculate the nucleotide and haplotype diversity for the Ukrainian site. For some sample locations we did not have the exact GPS coordinates ((?)) or we withhold the exact coordinates due to conservation status of *M. religiosa* in Germany, Austria, and Czech Republic ((§)). For some locations one (▲), two (▪) or three (•) individual(s) were excluded from the genetic analyses as they could not be completely aligned.

Region	No.	Π	H	Location	GPS	N	Haplotypes
Western France	1	0.0082	0.9091	Quincay	N 46.607 E 0.235(?)	11	*20(2), 22(2), 23, 24(3), 26, 27, 29*
Southeastern France	2	0.0025	0.9872	Bollène	N 44.252 E 4.803	3	*108, 109, 110*
				Pouzol, Ornac-l'Aven	N 44.316 E 4.419	2	*108, 118*
				Ornac-l'Aven	N 44.301 E 4.419	2	*112, 117*
				Labastide-de-Virac	N 44.352 E 4.403	1	*120*
				Sérignan-du-Comtat	N 44.187 E 4.838	6	*111, 112, 113(2), 115,* ▲
Eastern France	3	0.0078	1.0000	Chagny	N 46.903 E 4.739	13	*23, 56(3), 59, 61(2), 62, 64, 67, 68,* ▪
	4	0.0004	0.9111	Jaillon	N 48.755 E 5.963	6	*52(2), 53,* •
	5	0.0101	1.0000	Montenach	N 49.424 E 6.371	5	*46, 47, 48, 49,* ▲
	6	0.0075	1.0000	Blotzheim	N 47.603 E 7.510	10	*69, 70, 71, 72, 73, 74, 75, 76, 77, 78*
Western Germany	7	0.0076	0.5238	Glottertal	N 48.049 E 7.942(§)	8	*85(2), 1W(5),* ▲
				Schelingen	N 48.104 E 7.683(§)	4	*20,* •
	8	0	0	Weyher	N 49.268 E 8.084(§)	13	*1W(13)*
				Pleisweiler-Oberhofen	N 49.116 E 8.003(§)	1	*1W*
	9	0	0	Heppenheim	N 49.642 E 8.638(§)	5	*20(5)*
Eastern Germany	10	-	-	Geiseltalsee	N 51.308 E 11.890(§)	2	*100(2)*
	11	-	-	Silz (a.d. Müritz)	N 53.519 E 12.440(§)	1	*44*

- continued on next page -

- Table 2.1 continued from previous page -

Region	**No.**	**Π**	**H**	**Location**	**GPS**	**N**	**Haplotypes**
Eastern Germany	12	0.0005	0.5556	Berlin (Schöneberg)	N 52.482 E 13.366(§)	6	*38(6)*
				Berlin (Biesdorf Süd)	N 52.499 E 13.546(§)	3	*141, 142(2)*
	13	0.0010	1.0000	Sedlitzer See	N 51.549 E 14.104(§)	3	*95, 96, 97*
	14	0.0003	0	Nochten	N 51.431 E 14.599(§)	7	*31(7)*
Czech Republic	15	0.0014	0.6857	Prevov nad Labem	N 50.158 E 14.823(§)	5	*44(2), 156(3)*
				Žehuň	N 50.134 E 15.291(§)	10	*148(8), 165(2)*
	16	-	-	Krňovice	N 50.191 E 15.979(§)	1	*162*
				Hradec Králové	N 50.209 E 15.830(§)	1	*161*
	17	-	-	Litovelské Pomoraví	N 49.720 E 17.013(§)	1	*163*
				Slatinky	N 49.547 E 17.094(§)	1	*164*
Austria	18	-	-	Retz	N 48.757 E 15.954(§)	1	*147*
	19	0.0021	1.0000	Baden	N 48.002 E 16.231(§)	1	*145*
				Brunn am Gebirge	N 48.109 E 16.286(§)	1	*146*
				Mödling	N 48.082 E 16.286(§)	1	*98*
				Perchtoldsdorf	N 48.120 E 16.269(§)	1	*140*
Slovakia	20	-	-	Kosorín	N 48.649 E 18.808(?)	2	*176, 177*
	21	-	-	Zemplínská Šírava	N 48.799 E 22.066(?)	1	*178*
Hungary	22	-	-	Győr	N 47.687 E 17.645(?)	1	*174*
	23	0.0027	1.0000	Örkény	N 47.129 E 19.430(?)	1	*175*
				Kunpeszer	N 47.061 E 19.278(?)	6	*167, 168, 169, 171, 172,* ▲
	24	-	-	Zalaszentmihály	N 46.729 E 16.948(?)	1	*173*
Northern Italy	25	0.0002	0.6000	Mont Grappa	N 45.802 E 11.743	7	*1, 2(3), 4(3)*
	26	0.0010	0.7143	Castiglione delle Stiviere	N 45.392 E 10.513	6	*14(4), 15, 17*
	27	0.0023	0.9333	Aosta Valle	N 45.733 E 7.313(?)	6	*8, 9(2), 11, 12, 13*
Ukraine	28	-	-	Kaniv	N 49.755 E 31.461(?)	2	*91,* ▲
				Cherkasy	N 49.441 E 32.064(?)	1	*94*
				Mykolaiv	N 46.967 E 31.981(?)	1	*93*

Abbreviations: No., site numbers as given in Fig. 2.1; Π, mean nucleotide diversity between sequences at sampled site (p-distance, calculated in MEGA, version 5; Tamura et al. 2011); H, haplotype diversity at sampled site (calculated in Arlequin, version 3.5.1.3; Excoffier & Lischer 2010); GPS, coordinates of sampled individuals or of locations near sampled individuals; N, number of individuals sampled; Haplotypes, determined mtDNA haplotypes of combined alignments of genes COI, COII, Cyt b, and ND4 with counts of referring haplotype in each location (in brackets).

2.3.3 Molecular analysis

For DNA-isolation, we extracted DNA from all tissue samples using the High Pure PCR template preparation kit, following the manufacturer's protocol (Roche Diagnostics GmbH, Mannheim, Germany). Polymerase chain reactions were performed using PuReTaq Ready-to-Go PCR Beads (GE Healthcare Lifescience, Freiburg, Germany). The final volume of 25 µl contained 1 µl DNA extraction solution, 1 µl each of forward and reverse primer (10 pmol μl^{-1}) and 22 µl HPLC graded water. We partially sequenced four mitochondrial genes: cytochrome c oxidase subunit 1 (COI), cytochrome c oxidase subunit 2 (COII), cytochrome b (Cyt b) and NADH dehydrogenase subunit 4 (ND4). To obtain a long fragment of ND4 we used two primer pairs. Forward and reverse primers, references and amplification protocols for COI, COII, Cyt b and ND4 are given in Online Resources 2.1 and 2.2.

We purified positive PCR products with the High Pure PCR Product Purification Kit, following the manufacturer's protocol (Roche Diagnostics GmbH). After a re-examination of the purified PCR product on a 1.02% agarose gel under UV light, we used the positive PCR products for single stranded sequencing.

For the Sanger dideoxy method, the final volume of 10 µl contained 1 µl purified PCR product, 1 µl primer, 1 µl Big Dye Terminator v3.1 (Applied Biosystems, CA, USA), 2 µl buffer and 5 µl HPLC graded water. The amplification protocol for the Sanger dideoxy method is provided in Online Resource 2.2. After gel filtration with Sephadex G-50 Medium and DNA stabilisation with HiDi Formamide (Life Technologies GmbH, Darmstadt, Germany), we analysed the sequencing reactions using an automatic capillary sequencer ABI 3130xl Genetic Analyzer (Hitachi/ Applied Biosystems). For each gene we analysed, the forward and the reverse sequence of at least eight randomly sampled individuals were used to construct a reference sequence. One-stranded sequences were compared to these reference sequences in case of ambiguity. All genes, except for ND4, provided genetic information when reading from both ends of the sequences so we continuously sequenced forward and backward. Only one fragment of ND4 (primer Mant_ND4_1.9a) was from here on sequenced one-stranded. The COII and Cyt b sequences of 26 individuals from central Europe were kindly provided by P. Janšta (unpublished data).

2.3.4 Population genetic analysis

The sequences obtained by us were aligned to their complements using the software Sequence-Navigator (version 1.0.1, Applied Biosystems) and refined by eye.

In order to check whether the four analysed genes evolved similarly (Ballard & Kreitman 1995), we constructed for each gene a maximum parsimony tree by close neighbour-interchange on random trees in MEGA (version 5; Tamura et al. 2011; results not shown). We checked tree topology by comparing the pairwise genetic distances of haplotypes for all genes in and between each resulting genetic cluster (central European major sub-cluster, central European minor sub-cluster, and west European cluster, see Results) in a Mantel test (SsS version 1.1k, Rubisoft Software GmbH). We excluded the sequence data of the outgroup cluster Ukraine (east European cluster) from these calculations because these haplotypes were statistically highly influential but uninformative for tree topologies within our focal study region. Each of the clusters was represented in this test by its three most divergent individuals. The pairwise genetic distances of haplotypes were calculated using the Tamura & Nei substitution model with γ-parameter α = 0.05 (Tamura & Nei 1993). This model fitted best for the samples taken from all genes and was determined based on the AIC criterion (Akaike Information Criterion, Akaike 1979) in MEGA (version 5; Tamura et al. 2011). Additionally, we conducted a partition homogeneity test to determine whether the individuals were assigned, based on their haplotypes, to the same clusters for all genes (Bull et al. 1993). Here we again compared the three most divergent haplotypes of each cluster and ran heuristic searches with 10 000 replicates in PAUP* (Swofford 2003).

To estimate genetic similarity or dissimilarity between all European haplotypes, we calculated neighbour joining trees based on the Tamura 3-parameter substitution model with the estimated γ-parameter α = 0.49 (Tamura 1992) and maximum parsimony trees using the program MEGA (version 5; Tamura et al. 2011). Bootstrap values of trees were assessed with 2 000 replicates.

To determine the sources of German *M. religiosa* populations, we defined groups of European populations by a spatial analysis of molecular variance based on the genetic variance within and between populations (software SAMOVA; Dupanloup et al. 2002). This approach identifies groups of populations that are geographically adjacent and genetically similar. For the SAMOVA we assigned the individuals from the 44 geographical locations to 28 geographical sites based on the distances between the locations where they had been sampled in field (Table 2.1). Each site consists of all individuals from locations sampled within a distance smaller than 50 km (except for Ukraine). As we conducted the SAMOVA with all sites having more than one individual (Table 2.1) we pooled the three individuals from the three Ukrainian populations into a single site. We used 100 random start configurations and stepwise increased the number of groups (K) until a maximum genetic differentiation among the groups was reached (FCT maximized). The analysis was run for K = 2 to K = 5 groups because the maximum genetic differentiation was reached with K = 3. The significance of the fixation index was tested with 1 023 permutations.

To assess whether *M. religiosa* is currently expanding its range into Germany by immigration from adjacent countries, we studied the current range dynamics of *M. religiosa* in Europe from mismatch distributions and Tajima's D and Fu's Fs values. For the mismatch distribution analysis, we generated two populations: a west European population (all sequenced individuals from western France and western Germany, N = 79, Table 2.1) and a central European population (all central European, Italian, and east German individuals, N = 77, Table 2.1). These two populations were based on the two major clusters containing German haplotypes that were corroborated by the phylogenetic tree and SAMOVA (Figs. 2.1, 2.2, see Results). All individuals from the Ukraine were excluded from this analysis (N = 3, Table 2.1). For the remaining two populations we compared the observed mismatch distributions to the standard models of spatial and demographical expansions applying the software Arlequin (version 3.5.1.3; Excoffier & Lischer 2010). We tested both expansion models (spatial and demographical expansions) since an observed mismatch distribution may be caused by more than just one population process (Excoffier 2004). We conducted 1 000 bootstrap repetitions in this analysis.

To determine whether the found genetic lineages evolved under random processes (infinite site model), we analysed the distribution of mtDNA sequence variations within the western and central European population. We therefore calculated Tajima's D and Fu's Fs in Arlequin (version 3.5.1.3; Tajima 1989; Fu & Li 1993; Excoffier & Lischer 2010). Besides selective effects, significant Tajima's D values can be caused by population expansion, bottlenecks, or heterogeneity in mutation rates (Tajima 1996). Apart from that, Fu's Fs is very sensitive to population demographic expansion (Fu 1997).

2.4 Results

In total, we successfully sequenced 158 out of 171 individuals for 3 435 bp (810 bp COI; 755 bp COII; 745 bp Cyt b; 1 125 bp ND4) of which we could unambiguously determine 3 304 bp.

Among the four genes studied, maximum parsimony and neighbour-joining trees showed similar topologies. Overall, the evolution of all genes was correlated (mantel tests: COI and COII: P = 0.007; COI and Cyt b: P = 0.006; COI and ND4: P = 0.006; COII and Cyt b: P = 0.002; COII and ND4: P < 0.001; Cyt b and ND4: P = 0.007). The partition homogeneity test carried out for all four genes COI, COII, Cyt b and ND4 revealed evolutionary congruence (p = 0.461), indicating that the four genes evolved similarly. Based on these results, we combined the alignments of all four genes into one single alignment per individual (COI – COII – Cyt b – ND4) for further phylogeographic analyses. This yielded 87 different haplotypes with a total of 234 polymorphic sites.

2.4.1 Genetic relationships

The gene tree, obtained from the neighbour-joining approach (Tamura 3-parameter method, γ-parameter α = 0.49; bootstrap 2 000 repetitions) revealed three distinct clusters, all of which were supported by bootstrap values greater than 80%. The distribution of the haplotypes coincided with their geographic distribution, corresponding to three European biogeographic regions. The first cluster represented the outgroup Ukraine, hereafter called East lineage (for east European lineage). The second cluster included all central European, Italian, and east German haplotypes, hereafter called Central lineage (for central European lineage). The second cluster had two sub-clusters (statistically supported with bootstrap values greater than 80%), one major, which included all central European and Italian individuals and one minor sub-cluster, which included individuals from France and western Germany (haplotypes 20, 24, 47, 49, 56, 75, 77, 85, Table 2.1). The third cluster was comprised of the French and west German haplotypes, hereafter called West lineage (for west European lineage; Fig. 2.2). Identical haplotypes were found for a west German and French (haplotype 20, Table 2.1) as well as for an east German and Czech location (haplotype 44, Table 2.1). The subdivision found in the second cluster most likely depicts a past population mixture of populations from the Central lineage (most probably derived from Italy) and populations from the West lineage (Fig. 2.1(a)) in France. No mixture of the East lineage with any other described lineages was found.

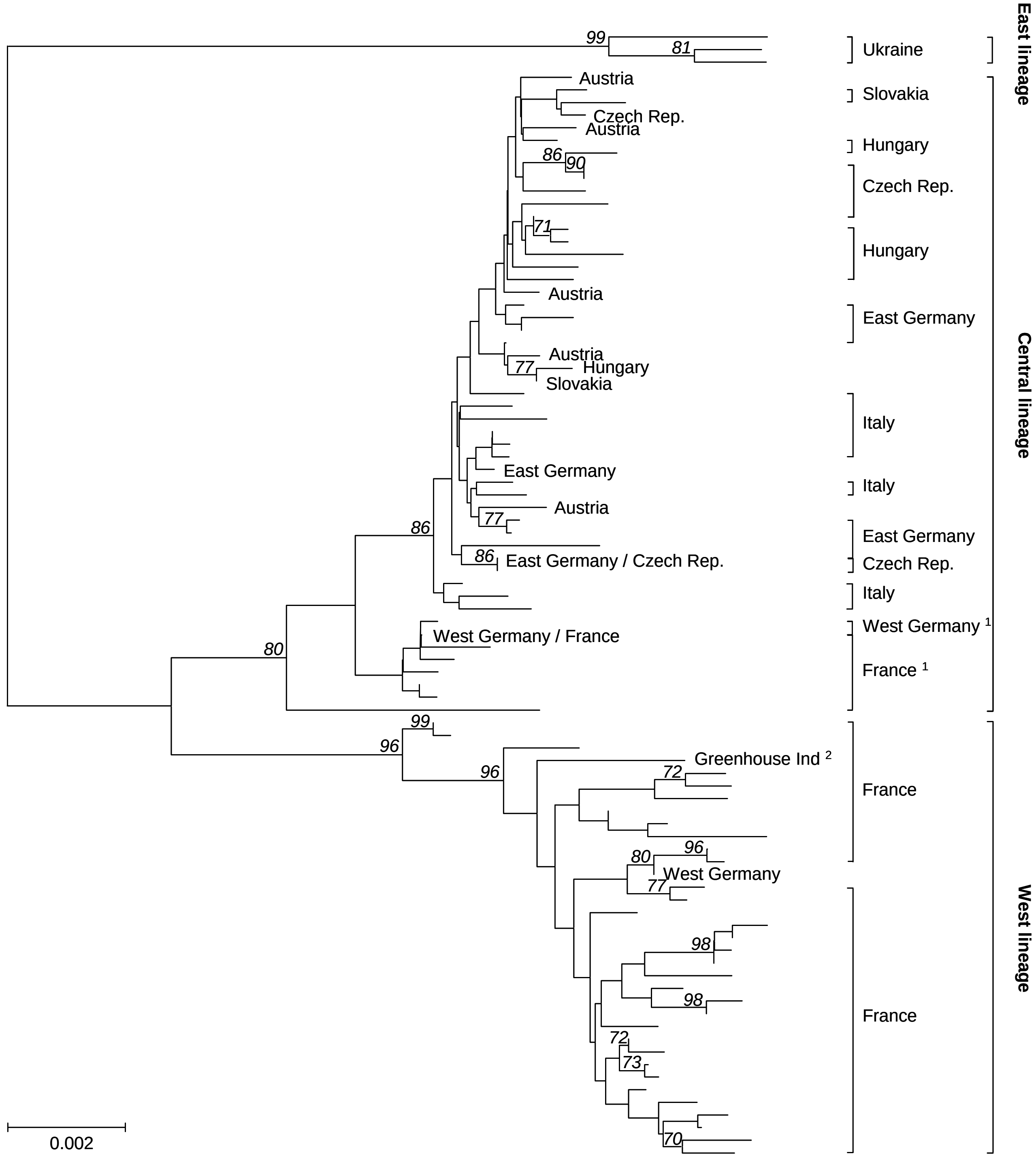

Fig. 2.2. Neighbour-joining tree calculated from the combined sequences of mitochondrial genes COI, COII, Cyt b and ND4. The tree was derived using a Tamura 3-parameter model with γ-parameter α = 0.49 for 87 *M. religiosa* haplotypes. Bootstrap values, indicating a support over 70% in 2 000 bootstrap replicates are shown above branches. [1] Some haplotypes of the Central lineage were found in western Germany and France (minor sub-cluster). [2] The haplotype Greenhouse Ind belongs to an individual, which was accidentally introduced from France to Germany (found in a greenhouse) and is assigned to France based on its haplotype.

A total of 207 most parsimonious trees revealed the same clustering (bootstrap 2 000 repetitions; tree length = 393; consistency index = 0.508; retention index = 0.919), which indicates a high statistical support for the gene tree (Online Resource 2.3).

The spatial analysis of molecular variance (SAMOVA 1.0; Dupanloup et al. 2002; Fig. 2.1(a), Table 2.2) also supported the partitioning of haplotypes into the three major European groups (East lineage, Central lineage, West lineage, Fig. 2.2). The maximum variation among groups (FCT) was reached with the classification of three groups: the differences in the FCT index between two and three groups (8.5%) was considerably higher than between three and four groups (0.2%). Finer groupings (K > 3) did not further change the FCT. A SAMOVA excluding the outgroup Ukraine (east Europe) revealed the same genetic clustering of the remaining two clusters (Online Resource 2.4).

Table 2.2. First three groupings obtained from the spatial analysis of molecular variance (SAMOVA). The percentage of total variance (%) that is explained by the grouping as well as the fixation indices are shown. Groups [ ] comprise all individuals of the named lineage. Group [Heppenheim] is made up of individuals from Heppenheim (western Germany), all of which had the same haplotype 20. Significance level * P < 0.05, *** P < 0.001.

Groups	Source of variation	Variance (%)	Fixation index
2			
[Eastern Europe]	Among groups	57.89	$F_{CT} = 0.5789$*
[Central, Western Europe]	Within populations	15.67	$F_{ST} = 0.8433$***
	Among populations within groups	26.44	$F_{SC} = 0.6278$***
3			
[Eastern Europe]	Among groups	62.12	$F_{CT} = 0.6213$***
[Central Europe]	Within populations	25.41	$F_{ST} = 0.7459$***
[Western Europe]	Among populations within groups	12.46	$F_{SC} = 0.3291$***
4			
[Eastern Europe]	Among groups	62.26	$F_{CT} = 0.6226$***
[Central Europe]	Within populations	26.11	$F_{ST} = 0.7389$***
[Western Europe]	Among populations within groups	11.63	$F_{SC} = 0.3082$***
[Heppenheim]			

Mismatch distributions, created separately for both the west and the central European population, clearly indicated an expansion of both populations within Europe (Fig. 2.3; Harpending 1994). Within the west European population, a bimodal mismatch distribution of the observed number of differences between all pairs of sequences indicated the population mixture of the West lineage and the minor sub-cluster of the Central lineage. When excluding individuals belonging to the central minor sub-cluster, the reduced west European population showed a unimodal mismatch distribution. Mismatch distributions of both European populations did not deviate from the spatial expansion model (H_0: estimated parameters are true, west European population: P = 0.219; central European population: P = 0.485), nor from the demographical expansion model (H_0: estimated parameters are true, west European population: P = 0.156; central European population: P = 0.223).

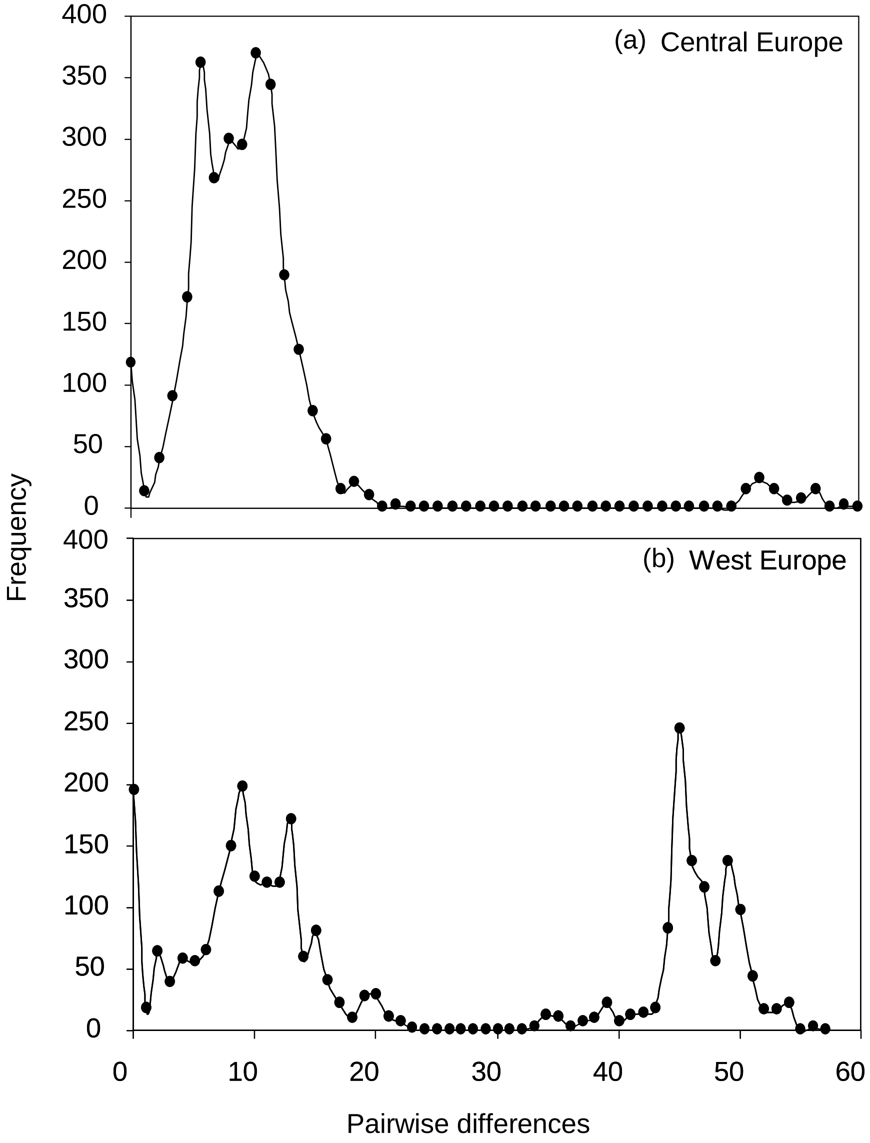

Fig. 2.3. Observed distributions of pairwise differences between sequences (mismatch distributions) in (a) central Europe and (b) western Europe. In the central European population the created mismatch distribution was unimodal whereas in the west European population the mixture of the West and Central lineage (sub-cluster) caused a bimodal distribution pattern.

Tajima's D and Fu's Fs were significantly negative in the central European population (D = -2.232, P = 0.001; Fs = -23.226, P < 0.001). The west European population showed no significant departure from the infinite site model (D = 0.176, P = 0.681; Fs = -6.924, P = 0.084). When excluding individuals belonging to the central minor sub-cluster, the smaller west European population showed a marginally significant trend towards a negative departure from the infinite site model (D = -1.392, P = 0.061; Fs = -16.260, P = 0.002). The significantly negative Fu's Fs values of the west and the central European population clearly supported the hypothesis of demographic expansion. Hence, the unimodal mismatch distributions derived for both major European populations suggest that negative D and Fs values more likely result from recent demographic expansions (Rogers & Harpending 1992) than from selection.

2.5 Discussion

Quite a few records of *M. religiosa* exist for Germany (Fig. 2.4(a); summarised in Berg et al. 2011). Most of these populations exist or have existed in spatially restricted areas. Populations are small, quite unstable and often vanish after a short period of time (Berg et al. 2011). Such colonisations and extinctions are frequent at the edge of a species distribution: despite continuous colonisation, only a few populations, which successfully colonise species-specific optimal habitats, become stable (Pulliam 2000).

2.5.1 Phylogeographic analyses

To understand from which geographic regions the German *M. religiosa* populations descended, we analysed the genetic structure of European *M. religiosa* populations. Phylogeographic analyses of four mitochondrial genes (COI, COII, Cyt b, ND4) revealed a highly resolved gene tree (3 304 bp) and a clear geographical partitioning of the sampled European *M. religiosa* individuals. Further evidence for the high reliability of our results is the correct assignment of an anthropogenically displaced individual ("Greenhouse Ind", Fig. 2.2), found in a greenhouse in Germany, to its state of origin in France, based on its haplotype.

2.5.2 Genetic clusters of M. religiosa populations in Europe

Within Europe, we found three major genetic clusters of *M. religiosa*, each of which coincided with their current geographic distribution: the East lineage consists of haplotypes of the outgroup Ukraine, the Central lineage of haplotypes mainly found in central Europe but also in western Europe (minor sub-cluster), and the West lineage of haplotypes found only in western Europe (Figs. 2.1, 2.2). Taberlet et al. (1998) and Hewitt (1999) reviewed similar geographically distinct genetic clusters for several other species within Europe. This clustering reflected genetic isolation by distance during glacial periods (Hewitt 1999): major ice age refugia were located in the Balkans, in southern east Europe (Ukraine, Russia), the Iberian Peninsula and Italy. After the ice melted, northern parts of Europe were re-colonized primarily from these areas (Taberlet et al. 1998; Hewitt 1999).

However, a detailed phylogeographic analysis of glacial refugia and range change during glacial and inter-glacial periods is beyond the scope of this paper and will be addressed by Janšta (in prep.).

2.5.3 Relationship of German M. religiosa

Regarding our hypotheses on the origin of German *M. religiosa,* we identified individuals within Germany clustering either to the Central lineage or the West lineage. East German populations were strongly genetically related to the populations of the Central lineage and west German populations were strongly related to the populations of the West lineage. The East lineage was not relevant for colonising Germany.

Within west German and French populations we found individuals clustering to the Central lineage (minor sub-cluster, Figs. 2.1, 2.2), which suggests that these western individuals descended from the Central lineage. However, these individuals were still genetically distinct from individuals of central European populations (Fig. 2.2), suggesting that the populations of the West and Central lineage mixed in France during a previous interglacial period. The Central lineage seems to have expanded from northern Italy into France, resulting in mixed populations of both lineages. Cooper et al. (1995) and Lunt et al. (1998) also observed for the grasshopper *Chorthippus parallelus* a range expansion of central European lineages, resulting in a mixture of genomes during a previous interglacial and blocking later Italian genome expansion (Hewitt 1999). Also other animal and plant species had similar expansion patterns (Hewitt 1999). Further explanations for a population mixture in France of the West and Central lineage is beyond the scope of this paper.

2.5.4 Immigration of M. religiosa into Germany

As presumed, *M. religiosa* immigrated from two directions into Germany. West German populations originated from eastern France, and most likely reached Germany via the climatically favourable migration route Burgundy Gate in eastern France and/ or the Moselle Valley (Brechtel 1996; Detzel & Ehrmann 1998; Berg et al. 2011; Fig. 2.4(a)). These routes are the major routes linking southern Europe to central Europe during the postglacial range expansion of many animal and plant species (Detzel 1995) as they connect Mediterranean habitats with German temperate habitats.

East German *M. religiosa* populations originate from central European populations. Species from southeastern and eastern Europe commonly migrate into Germany through Poland and the Czech Republic (central Europe), specifically via the Polish/ north German lowlands and the Elbe valley in Saxony (Detzel 1995; Bylebyl et al. 2008). As the geographically closest known populations of *M. religiosa* in central Europe are found in the Czech Republic, individuals from central European *M. religiosa* populations most likely migrated from the Czech Republic into eastern Germany. The potential migration route Elbe Valley (Fig. 2.4(a)) connects plains in Ústí, Czech Republic and Lower Saxony, Germany.

Among others, these migration routes into Germany have also been detected in studies on postglacial expansion for various other species (Taberlet et al. 1998; Hewitt 1999; Bylebyl et al. 2008). Cooper et al. (1995) found for the grasshopper *Chorthippus parallelus* only one postglacial migration route from central Europe into Germany. Detzel (1995) also described a unidirectional migration route for the locust *Locusta migratoria*, which presumably migrated via the Donau delta into Germany. The grasshopper *Platycleis tessellata* and the cricket *Meconema meridionale* reached Germany from western localities via the Burgundy Gate. Western and eastern migration routes into Germany are presumed for the grasshoppers *Aiolopus thalassinus* and *Polysarcus denticauda* (Detzel 1995). In total, our postglacial range expansion model derived for *M. religiosa* in Germany is consistent with studies on grasshoppers, locusts and crickets.

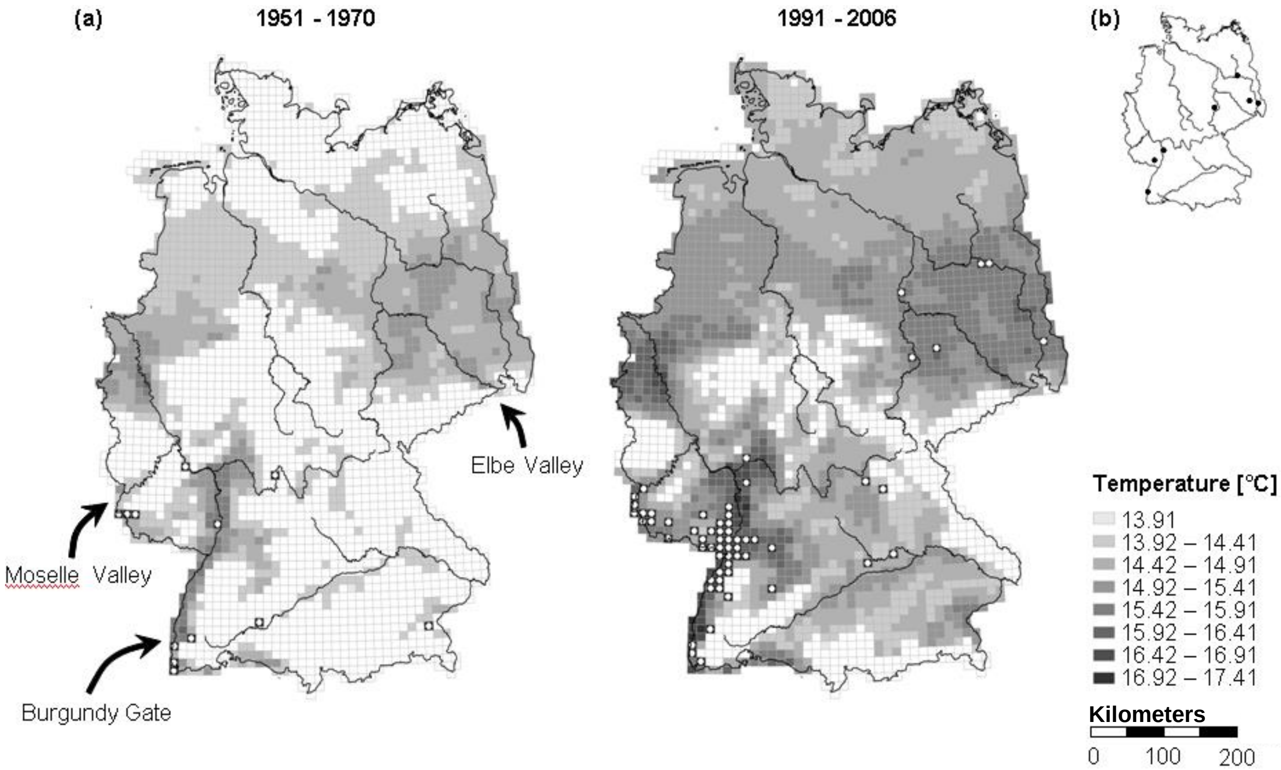

Fig. 2.4(a). Mean summer temperature (May-October, in [°C]) in Germany for two time periods (1951-1970 and 1991-2006; Badeck et al. 2008) at the resolution of ordinance survey maps (1:25 000, ca. 10 x $10\ \text{km}^2$). The threshold of 13.91°C was derived from the mean temperature of grid cells in which *M. religiosa* was recorded until 1970. Black squares with white circles represent records of *M. religiosa* for 1970 and 2006, respectively (Berg et al. 2011). With proceeding time, temperature and records increased (Ehrmann 2003; Liana 2007; Berg et al. 2011). As *M. religiosa* is tolerant to winter temperatures even below -24°C (100% egg mortality in ootheca at -42°C; Salt & James 1947), which are rarely observed in Germany, we hypothesise that increasing summer temperatures contribute to the current range expansion of *M. religiosa*. (b) Populations sampled in Germany for genetic analyses.

The nucleotide and haplotype diversity within German *M. religiosa* populations was strikingly small compared to other *M. religiosa* populations in surrounding European countries (Table 2.1). Such reduced nucleotide and haplotype diversity can result from spatial expansion if a small number of pioneering individuals, which originate from populations at the edge of the species distribution, established new populations (Taberlet et al. 1998; Hewitt 1999; Dlugosch & Parker 2008). In extreme cases, one single female of *M. religiosa* can establish a new population with a single haplotype (Berg et al. 2011), as it can reproduce under facultative parthenogenesis in the absence of males (Hideg 1996). A current range expansion of the west and central European *M. religiosa* populations is also supported by the mismatch distribution analysis and large negative Fs values (Rogers & Harpending 1992; Fu & Li 1993; Harpending 1994).

The distribution of records of *M. religiosa* and the hypothesised migration routes coincide with German regions showing the warmest summer temperatures (Fig. 2.4(a)). However, *M. religiosa* has not yet colonized all warm regions in Germany, presumably due to its low dispersal ability (Hideg 1994; Liana 2007). Furthermore, until today, west and east German *M. religiosa* populations have not mixed, yet. This reflects a clear longitudinal separation of thermally favourable regions in western and eastern Germany (Fig. 2.4(a)). We expect, under ongoing global warming and concomitant landscape changes that a longitudinal contact zone, as reviewed by Hewitt (1996) and Taberlet et al. (1998) will arise between the West and Central lineages.

2.6 Acknowledgement

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2.7 Supplementary material

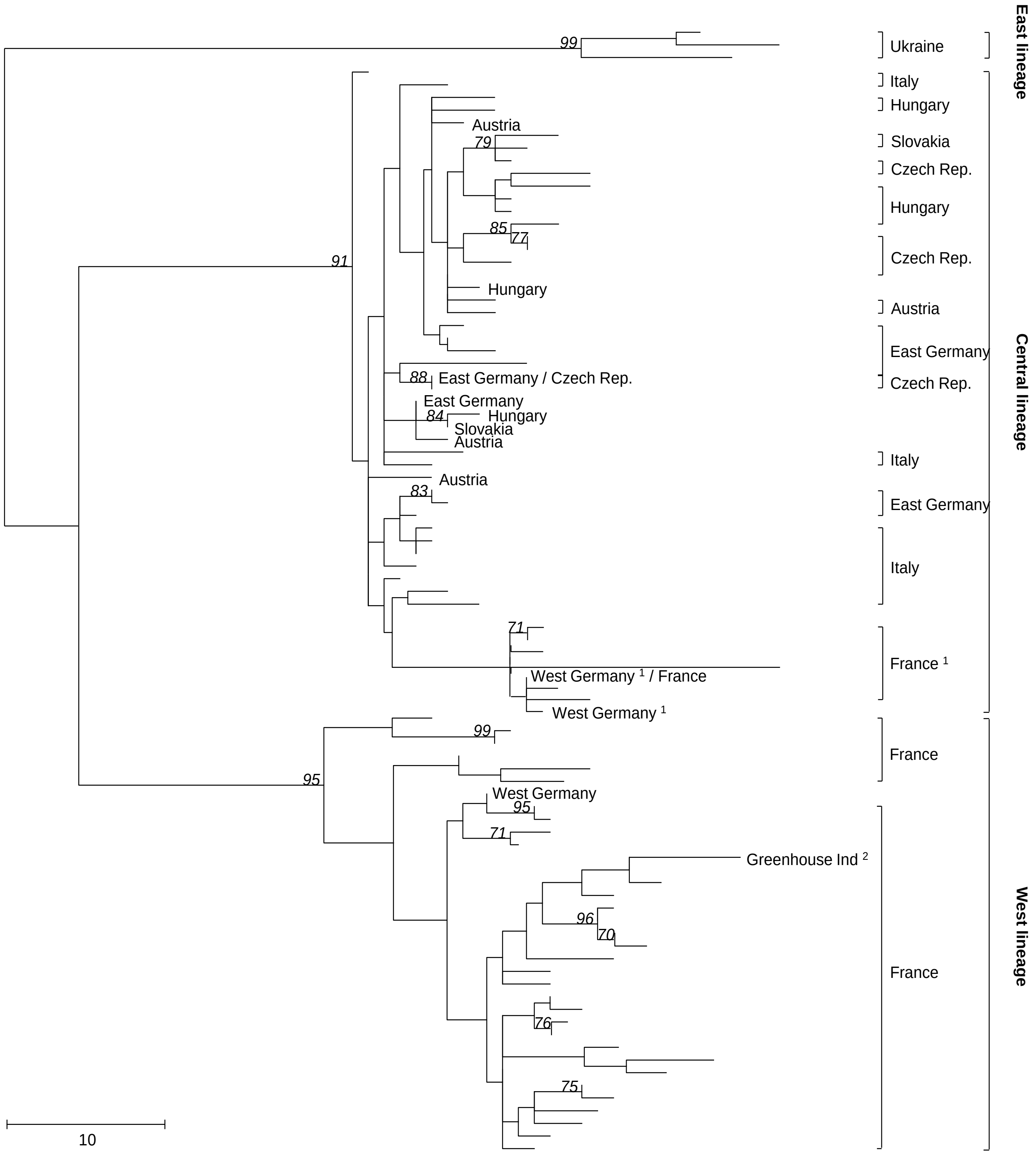
Online Resource 2.1. Primers used in amplification of COI, COII, Cyt b, and ND4.

Gene	Primer	Sequence of primer	Reference
COI	MT-C1-N2568 (f)	5'–GCTACAACATAATAAGTATCATG–3'	Brady et al. 2000
	MT-C1-J1718 (r)	5'–GGATTTGGAAATTGATTAGTTCC–3'	Simon et al. 1994
COII	COII-F-leu (f)	5'–TCTAATATGGCAGATTAGTGC–3'	Whiting 2002
	COII-9b (r)	5'–GTACTTGCTTTCAGTCATCTWATG–3'	Whiting 2002
Cyt b	CP1 (f)	5'–GATGATGAAATTTTGGATC–3'	Kergoat et al. 2004
	CB-N-11367 (r)	5'–ATTACACCTCCTAATTTATTAGGAAT–3'	Kergoat et al. 2004
ND4	Poly_ND4_F1 (f)	5'–TKCKGTWTGTGAAGGTGCTTTAGG–3'	Svenson & Whiting 2009
	Mant_ND4_2.0b (r)	5'–CCAGCTTGAAGACGTTCAGGTTGATATCC–3'	Svenson & Whiting 2009
	Mant_ND4_1.9a (f)	5'–GAAGGTAGATTAATTCCAACTTTATTTTTAA–3'	Svenson & Whiting 2009
	Mant_ND4_5b (r)	5'–CTCCTAATAAATTTAAAGAAGGAGGAG–3'	Svenson & Whiting 2009

Abbreviations: f, forward; r, reverse (Directionality for the primers corresponds to the direction of the gene.); COI, Cytochrome c oxidase subunit 1; COII, Cytochrome c oxidase subunit 2; Cyt b, Cytochrome b; ND4, NADH dehydrogenase subunit 4.

Online Resource 2.2. Amplification protocols used in polymerase chain reactions for COI, COII, Cyt b, ND4, and in the Sanger dideoxy method. For ND4 amplifications the protocols are dependent on the primer Mant_ND4_F1, which requires a lower annealing temperature than other ND4 primers (Svenson & Whiting 2009).

Primer	Hot start	Denature	Anneal	Extension	Final extend	Cycles
COI	94°C (2 min)	94°C (30 s)	47°C (30 s)	72°C (1 min 30 s)	-	35
COII	95°C (12 min)	94°C (1 min)	52°C (1 min)	72°C (1 min 15 s)	72°C (1 min)	40
Cyt b	92°C (5 min)	92°C (1 min)	48°C (1 min 30 s)	72°C (2 min)	72°C (10 min)	37
ND4 F1−2.0b	95°C (5 min)	95°C (30 s)	48°C (30 s)	72°C (1 min)	72°C (15 min)	55
ND4 1.9a−5b	95°C (5 min)	95°C (30 s)	54°C (30 s)	72°C (1 min)	72°C (15 min)	55
Sanger dideoxy method	96°C (1 min)	96°C (30 s)	45°C (15 s)	60°C (4 min)	-	25



Online Resource 2.3. Maximum parsimony tree for 87 *M. religiosa* haplotypes calculated from the combined sequences of genes COI, COII, Cyt b and ND4. Bootstrap support indices that were supported in over 70% of the 2 000 bootstrap replicates are shown above branches. [1] Some haplotypes of the Central lineage were found in western Germany and France. [2] The haplotype Greenhouse Ind belongs to an individual, which was accidentally introduced from France to Germany (found in a green house) and is assigned to France based on its haplotype.

Online Resource 2.4. First three groupings obtained from the spatial analysis of molecular variance (SAMOVA), excluding data from Ukraine (east Europe). The percentage of total variance (%) that is explained by the grouping as well as the fixation indices are shown. Group [Heppenheim] is made up of individuals from Heppenheim (western Germany), which all had the same haplotype 20. Group [Jaillon] is made up of individuals from Jaillon. Significance level *** P < 0.001.

Groups	**Source of variation**	**Variance (%)**	**Fixation index**
2			
[Western Europe]	Among groups	60.21	$F_{CT} = 0.6021$***
[Central Europe]	Within populations	26.63	$F_{ST} = 0.7337$***
	Among populations within groups	13.16	$F_{SC} = 0.3307$***
3			
[Western Europe]	Among groups	60.34	$F_{CT} = 0.6034$***
[Central Europe]	Within populations	27.37	$F_{ST} = 0.7263$***
[Heppenheim]	Among populations within groups	12.29	$F_{SC} = 0.3098$***
4			
[Western Europe]	Among groups	60.31	$F_{CT} = 0.6031$***
[Central Europe]	Within populations	27.83	$F_{ST} = 0.7217$***
[Heppenheim]	Among populations within groups	11.87	$F_{SC} = 0.2989$***
[Jaillon]			

3 HABITAT PREFERENCE OF GERMAN *MANTIS RELIGIOSA* POPULATIONS (MANTODEA) AND POTENTIAL CONSERVATION MEASURES

3.1 Abstract

In Germany, the thermophilic European mantid (*Mantis religiosa,* L.) is an endangered insect species. We studied habitat requirements of *M. religiosa*, essential to complete the life cycle within a year. We provide information on how to implement conservation measures for this species.

At two study sites in south western Germany, which were subject to conservation measures, we recorded structural and climatic conditions within different microhabitats. We also performed capture-mark-recapture experiments with adult *M. religiosa*, and mapped available microhabitats for adult roosting, ootheca deposition, ootheca hatching and imaginal molting. In order to assess structural and climatic preferences during the life cycle of *M. religiosa* we calculated the Lille habitat preference index and conducted logistic regression analysis for life phases.

Our results suggest that temperature is important for egg and larval development of *M. religiosa*. For egg deposition, females preferred solid substrates with high heat storing capacities (such as dry stone walls) as those attenuate the negative influence of cold weather periods on egg development. Being ambush predators, males and females preferred roosting sites with sufficient shelter and high prey abundance.

We suggest that mowing during the adult phase of *M. religiosa* should reduce vegetation height to a moderate level as this keeps prey abundance high. Mowing with a clearing saw or grazing over a short period in small fenced areas should be preferred over prolonged grazing, as grazers collaterally stamp down the vegetation. Grazers indirectly reduce prey availability as they deteriorate prevailing microclimatic conditions.

3.2 Introduction

Recent changes in climate and land-use induce range shifts of species in Europe (Parmesan et al. 1999; Walther et al. 2002; Sparks et al. 2007). As warm adapted species expand their range pole wards (Parmesan 2006), we currently observe an immigration of many Mediterranean species in central and northern Europe (Walther et al. 2009). Only in species-specific, environmentally adequate habitats can species survive and reproduce (Pulliam 2000).

The European mantid *Mantis religiosa* (L., 1758), a thermophilic insect species, is also expanding its range from Mediterranean and south eastern Europe into central Europe (Liana 2007; Walther et al. 2009; Berg et al. 2011; Linn & Griebeler 2015). At present *M. religiosa* inhabits thermally favourable areas in eastern (Berlin, Saxony) and south western Germany (Baden-Württemberg, Rhineland-Palatinate, Saarland; Berg et al. 2011).

As the distribution range margin of *M. religiosa* lies in Germany, growth of German *M. religiosa* population is strongly limited by environmental conditions (Hideg 1991; Liana 2007; Stärz et al. 2010). A further threat to *M. religiosa* in this country is the decrease of suitable habitats due to changes in land use (Brechtel 1996; Liana 2007). The threatened *M. religiosa* is protected by law in Germany (listed in the red list for Orthoptera as a category three species and particularly protected by law; BArtSchV, July 2009). It usually inhabits open dry landscapes such as fallow lands and meadows. In protected landscapes, such open grasslands are often conserved by mowing or grazing. However, mowing can also threaten the survival of *M. religiosa* by decreasing its population abundances (Braschler et al. 2009).

Liana (2007) and Stärz et al. (2010) conducted first studies on habitat requirements of *M. religiosa* in Poland and Germany. Liana (2007) found that the species prefers warm and sunny areas, whereas Stärz et al. (2010) observed differences in microhabitat use between the life stages oothecae (egg cases), larvae and adults in Germany. Even though both studies were extensive, they did not record temperature and relative humidity in microhabitats used by different life-stages. Hence, species-specific information on habitats enabling survival of *M. religiosa* is incomplete, although it is generally needed to identify suitable conservation measurements for species (Campbell et al. 1974; Wagner et al. 1985; Honek 1996).

In this study, we aimed at an understanding of microhabitats needed by the territorial *M. religiosa* to establish stable populations in Germany, and studied the impact of two different conservation measures on *M. religiosa* populations. We therefore investigated two stable *M. religiosa* populations that inhabit protected and managed sites located in western Germany. Over two growing seasons we investigated the microhabitats used during the life cycle of the species. We assume that the observation of its three life stages (larvae, adults, eggs) during one growing season in one area indicates that *M. religiosa* is able to complete its life cycle under the current habitat conditions.

We conducted capture-mark-recapture studies for adults, and we monitored available microhabitats for roosting Adults (hereafter used for resting, foraging or mating of adults) and for the three Life-History Events egg deposition, egg hatching, and imaginal molting (hereafter referred to as ALHE). In order to assess microhabitat preferences for each of the four ALHE, we further collected information on microhabitats (temperature, relative humidity, substrate, vegetation height), in which one or more ALHE was observed. Based on our field data we assessed microhabitat preferences of each ALHE using chi^2-goodness of fit test, the habitat preference index after Lille (1996, HPI) and logistic regression analyses. We expected to find a strong effect of temperature and humidity on each ALHE, as *M. religiosa* is a thermophilic species.

Mowing and grazing prevents bush encroachment and preserves open landscapes. Therefore, we expected that the two *M. religiosa* populations would benefit in terms of individual number and reproduction success from these conservation measures, which are regularly implemented in our study sites.

3.3 Material and Methods

3.3.1 Field work

3.3.1.1 Study species

Mantis religiosa is a generalistic predator insect species and is univoltine in Germany. At the end of the growing season females deposit egg cases (oothecae) on substrates (Berg et al. 2011). In Germany, all adult *M. religiosa* die after the first frost by the end of autumn. The species winters as egg in the spongy, well isolating oothecae (Hideg 1991). The ootheca protects the eggs from predation, physical damage, and climatic anomalies such as extremely cold temperatures (Hevers & Liske 1991). The lower lethal temperature for eggs sheltered in an ootheca ranges between -24° and -43°C (Salt & James 1947). After a diapause, larvae hatch from eggs in the following spring at warm temperatures. Larvae molt several times until they pass the imaginal molting in August.

3.3.1.2 Study sites

We studied two *M. religiosa* populations in south western Germany (Weyher, N 49.268 E 8.084 and Pleisweiler, N 49.116 E 8.003, Fig. 3.1) over a total period of two years (June 2011 – July

2013). Both sites were former vineyards and are now open dry fallow land. They are natural reserves and are located approximately 20 km apart from each other. The population studied in Weyher exists since 2005 (Himmler 2006) and in Pleisweiler since 2006, respectively (Röller 2007).

At each site, we surveyed a marked-out area and monitored environmental conditions on different substrates available in the areas. The marked-out study area in Weyher was smaller (ca. 144 m^2) than in Pleisweiler (ca. 352 m^2). Both sites were subject to conservation measures during our investigation period, ordered by the environmental authorities. Weyher was mowed twice with a clearing saw in 2011 (June/ July 2011, October 2011). Pleisweiler was grazed by sheep and goats for at least one week in July 2012.

3.3.1.3 Data collection of microhabitats

We divided each of the marked-out study areas in grid cells of 2 x 2 m (Fig. 3.1). Within each of the grid cells a mapping of the vegetation height (minimum vegetation height = *min veg height*, mean vegetation height = *mean veg height*, maximum vegetation height = *max veg height;* Table 3.1), and of found substrates (blank earth = *BE*; hard substrates = *HS*; woody plants = *WP*; herbaceous plants = *HP*; Table 3.1) enabled us to assess microhabitat preferences during the life-cycle of *M. religiosa*.

Measuring of temperature and relative humidity in grid cells started in July 2011 and ended in June 2013. Therefore, in total 33 data loggers (TGP-4500 and TGP-4505, Tinytag, Gemini Data Loggers, Chichester, UK) were installed in both study areas in order to hourly record temperature (in °C) and relative humidity (in %) on substrates *BE*, *HS*, *WP* and *HP* (Fig. 3.1). Data loggers were installed in Pleisweiler (Weyher) on the substrate *BE* at the ground (0 cm, 0 cm), on *HS* in heights between 0 and 85 cm above ground (0 and 133 cm), on *WP* in heights between 25 and 70 cm (5 and 20 cm), and on *HP* in heights between 0 and 30 cm (0 and 30 cm). The variability of data logger heights covered the range of substrate heights. Data loggers of the model TGP-4505 were used when the microhabitat was difficult to assess, because their sensors are located in an external probe with a 1.5 m long cable. With these data loggers temperature and relative humidity were measured directly at the surface of oothecae.

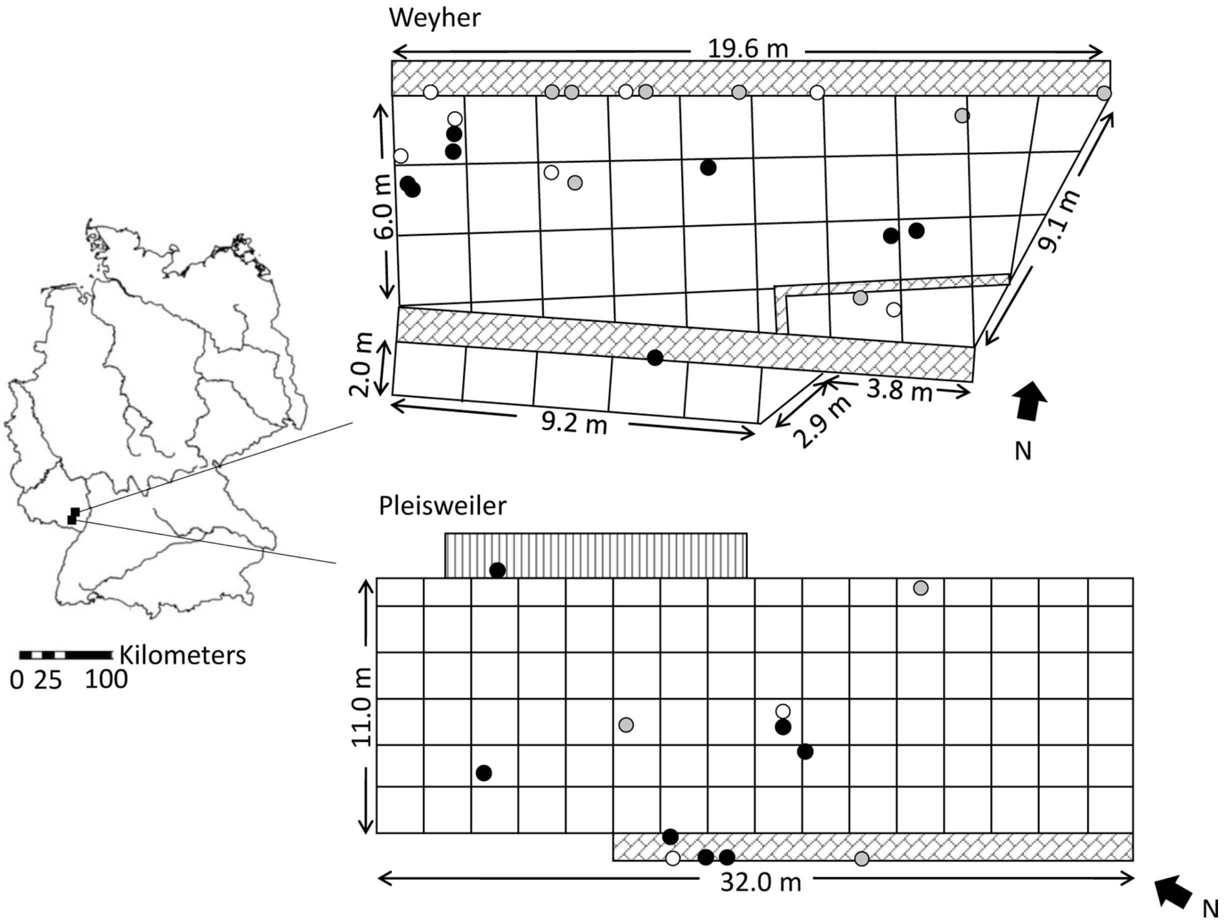


Fig. 3.1. Study sites Weyher and Pleisweiler in Germany. Shown are the marked-out study areas with grid cells of ca. 2 x 2 m, their size, major structures (bricked boxes: dry stone walls, lined box: pile of logs) and the position of data loggers (dots). Black dots indicate logger positions, where temperature and humidity were measured during the complete study period (2011-2013), white dots indicate positions, where temperature and humidity were measured in the time period 2011 to 2012, and grey dots indicate positions, where temperature and humidity were measured in the time period 2012 to 2013. We changed positions of data loggers between time periods according to new ootheca depositions.

During our study, we replaced damaged data loggers, and moved data loggers from hatched oothecae to newly deposited oothecae. At both study sites at least six data loggers were continuously installed in grid cells with different substrate types.

Table 3.1. Environmental variables and predictor variables used for modelling microhabitat preferences of ALHE of *M. religiosa.* Listed are environmental variables recorded in field, predictor variables derived and used for modelling and their abbreviations, as well as further descriptions of variables.

Environmental variables	**Predictor variables**	**Abbreviations**	**Further description**
vegetation height in grid cell	minimum vegetation height	*min veg height*	
	mean vegetation height^m	*mean veg height*	
	maximum vegetation height	*max veg height*	
study site	Pleisweiler = 1, Weyher = 2	*loc*	study site in which an ALHE was observed
study year	2011, 2012 or 2013	*year*	year in which an ALHE was observed
Julian day	day of observation	*day*	day within year at which an ALHE was observed (1 .. 365)
	day of ootheca deposition	$day_{(depos)}$	day within year at which a newly deposited ootheca was found (the deposition could have taken place maximal seven days before)
	day of ootheca hatching	$day_{(hatch)}$	day within year at which hatching remains on an ootheca were observed (hatching of larvae could have taken place maximal seven days before)
roosting or deposition substrate	*BE* = 1, *HS* = 2, *WP* = 3, *HP* = 4	*substr*	roosting or deposition substrate, respectively of ALHE; *BE* = blank earth, soil (without vegetation); *HS* = hard substrate, stones, dry stone walls, metal poles; *WP* = woody plants, logs, branches, small bushes, perennials; *HP* = herbaceous plants, grass, herbages
temperature	mean temperature of previous week^m	*temp*	mean temperature during week before an ALHE was observed on the substrate (°C)

^{m} predictor variables used for modelling computed from field data

3.3.1.4 Presence of adults and life history events

In order to assess microhabitats used by *M. religiosa* for adult roosting, and for the three life-history events egg deposition, egg hatching and imaginal molting (ALHE), we weekly controlled each grid cell of both marked-out study areas systematically. For each record, we noted the study site (*loc*), study year (*year*), and Julian day (*day*, $day_{(depos)}$, $day_{(hatch)}$; Table 3.1). Additionally, for adult roosting and for egg deposition we documented the substrate used (*substr*; Table 3.1).

To determine the roosting substrates and vegetation heights used by adult *M. religiosa*, we weekly performed individual based capture-mark-recapture experiments in both areas. We performed these experiments during the adult phase, which lasted from July to October in 2011 and 2012. We did not distinguish between immigrants and newly molted imagines as we assumed an open *M. religiosa* population for our marked-out areas showing equal rates of immigration into and emigration from the surrounding areas.

Simultaneously, we weekly recorded the deposition of ootheca between August and October in 2011 and 2012. Egg hatching was documented between May and July in 2012 and in 2013 by checking the ootheca for hatching remains (hereafter referred to as ootheca hatching).
In 2011 and 2012, we monitored imaginal molting between July and September by documenting the number of newly found, unmarked imagines, which were recorded during, or one week after the last larvae were recorded.

3.3.2 Statistical analyses: Modelling microhabitat preference of M. religiosa

3.3.2.1 Preparation of temperature and relative humidity data for analyses

For each data logger, we calculated daily mean temperatures and relative humidities. Therefore, their hourly recorded temperature and humidity values were averaged for each day.

For comparing the climatic conditions between different substrates, we averaged daily means of data loggers located on the same substrate, except for data loggers deposited close to the oothecae. For climatic conditions at oothecae, we used solely the records from the data loggers located close to them.

As we checked both areas only weekly, we calculated the arithmetic means for temperatures and relative humidities for the period between the day of the last check and the day at which we observed ALHE. These means are hereafter referred to as mean temperature of previous week (*temp*; Table 3.1) and mean relative humidity of previous week, respectively. The weekly means were used to test an effect of temperature and humidity on a substrate on the corresponding ALHE of *M. religiosa*.

The time period of oothecae hatching and larvae development (imaginal molting) differed strongly between both years. Hence, we additionally compared the mean spring (1 May – 30 June) temperature and humidity of each area and study year, calculated from the records of all data loggers of each area.

3.3.2.2 Analyses of environmental variables

We initially explored relations between environmental variables (Table 3.1) recorded in grid cells to identify independent predictor variables for further statistical analyses.

As daily mean temperature and relative humidity correlated over the entire study period (2011 - 2013; Spearman-Rank correlation: Weyher: $r_s = 0.658$, $P < 0.001$, $N = 803$; Pleisweiler: $r_s = 0.696$, $P < 0.001$, $N = 803$) and as insect development is mainly affected by temperature (Beck 1983), relative humidity was excluded from all following analyses.

We assessed the relation between Julian day (*day*) and daily mean temperature (averaged over all data loggers deposited in both study areas) by non-linear regression analysis using the formula given in Griebeler & Seitz (2007). This formula accounts for seasonal variability in mean temperature $T(t)$ during a year

$$T(t) = m\left(\sin\left(\frac{2\pi(t-p)}{365}\right)+1\right)+T_{\min} \quad (1).$$

Temperature correlated with Julian day (t) in terms of a successful fit of data to this formula ($SE_{\text{residual}} = 3.782$, df = 800). The displacement of the sine curve p was 111.558 Julian days ± 1.113 SE, the minimum temperature $T_{\min}$ was 1.549°C ± 0.241 SE and the amplitude of the sine curve m was 10.084°C ± 0.186 SE. The derived strong relationship between Julian day and temperature indicates that if Julian day is a good predictor of the presence of any ALHE of *M. religiosa* on a substrate, an effect of temperature (and relative humidity) is indirectly supported.

3.3.2.3 Habitat requirements for adults and life history events

Substrate preference of ALHE. In order to determine a preference of *M. religiosa* ALHE for any microhabitat (substrate) we applied chi^2-goodness of fit tests and calculated habitat preference indices (HPI) after Lille (1996). With the chi^2-goodness of fit tests we assessed whether the counts of ALHE on a substrate were only proportional to its availability in the study areas. The substrate *BE* was excluded in these tests because only one out of 389 ALHE was observed on this substrate. We were unable to conduct tests for imaginal molting due to an insufficient sample size for both populations in both study years, as well as for the deposition of ootheca in Pleisweiler in 2012.

We further calculated for both studied populations and both years (2011, 2012) different HPI (Lille 1996). These were derived from the relative frequencies of presences of adults and of ootheca deposition on substrates, respectively. The calculation of the HPI for ootheca hatching was redundant, as hatching larvae are bound to their ootheca and a female has chosen the location of the ootheca during its deposition in the previous year. The HPIs for imaginal molting were not calculated as we directly observed only eight out of 116 estimated imaginal moltings.

The HPI after Lille (1996) is given by formula

$$HPI = \log \frac{N[\%]}{\sqrt{A[\%]}} \qquad (2),$$

where *N* is the percentage of usage of a certain substrate, and *A* is the percentage of this substrate available within the study site. HPI = 0 indicates an area proportional usage of a substrate. For *N* = 0 HPI is undefined but suggests a strong avoidance of this substrate.

Modelling microclimatic preferences of ALHE with logistic regression. In order to test the effect of environmental predictor variables on each ALHE, we carried out logistic regression analysis using a stepwise forward approach. We only used binary models (presence-absence data) as our datasets on ALHE were too small to study the effect of environmental parameters based on the frequency of each of the ALHE. For adult roosting and for ootheca deposition, data obtained in both study areas and in 2011 and 2012 were pooled into one large datasets in order to increase the dataset on each ALHE. For ootheca hatching, data obtained in both study areas in 2012 and 2013 were pooled into one dataset. For imaginal molting no reliable models could be established, because the data set was still too small after pooling. Finally, we successfully build logistic regression models only for adult roosting, ootheca deposition and ootheca hatching.

In the logistic regression models, the predictor variable *temp*, the control variables *day*, *year*, and the variable *loc* were tested. Furthermore, variables of the grid cells where we observed individuals were tested. The latter were *min veg height*, *max veg height*, and *mean veg height* as well as *substr*. The variable *substr* coded substrates by numbers reflecting an increasing vegetation density (*BE* = 1, *HS* = 2, *WP* = 3, *HP* = 4; Table 3.1). Only for ootheca hatching two further predictor variables $day_{(depos)}$ and $day_{(hatch)}$ were considered. Predictor variables tested are summarised in Table 3.1.

Before conducting the logistic regression analyses for ALHE, we checked for pairwise correlations between potential predictor variables. Linear correlating parameters with $r_s \geq 0.7$ were a-priori excluded as potential predictors (Dytham 2011).

We identified candidate logistic regression models for each ALHE based on their significant deviation from the null model, and based on the criterion that they were not affected by over or under dispersion (phi between 0.8 and 1.2). To test whether models derived for an ALHE differ from the null model we conducted chi^2-goodness of fit tests as implemented in the package ‘stats’ (version 2.14.2, R). We used this software also to assess model over or under dispersion. From the candidate models the final model for each ALHE was chosen according to its AIC value (Akaike Information Criterion, Akaike 1979; lowest AIC value, Burnham & Anderson 2004). The goodness-of-fit of all models was identified from Nagelkerke’s R^2 (R^2_N; package ‘fmsb’, version 0.3.8, R). In our logistic regression analyses we used the standard settings for general linear models (glm, package ‘stats’ version 2.14.2, R) and assumed binomially distributed errors.

3.3.3 Effect of conservation measures

In order to examine the effects of conservation measures in our two study areas on the most common substrate *HP* (Weyher 45.0%, Pleisweiler 80.3%; Fig. 3.2) we conducted chi^2-tests. We compared daily mean temperatures recorded on *HP* after conservation measures took place with temperatures, expected if conservation measures would have been absent. These expected mean temperatures were derived from fitting temperatures measured before and after the conservation measure to formula 1. We assumed in this analysis that an effect of the conservation measure is negligible when the new vegetation period starts (defined as 1 April of following year). Thus, for Weyher differences between daily mean temperatures observed and expected between 20 July and 25 October 2011 and for Pleisweiler temperatures between 7 August and 25 September 2012 were examined for *HP*.

3.3.4 Software

All regression and correlation analyses were carried out in the software R (version 2.14.2, R Core Team 2012). Chi^2-goodness of fit tests were conducted in STATISTICA (version 5.1, StatSoft Inc.) and in the software R. Further statistical tests were computed with the software SPSS Statistics (IBM, version 21).

3.4 Results

3.4.1 Field work

3.4.1.1 Life cycle stages

In total, we captured 316 times adult *M. religiosa* in both study areas during both study periods. Population sizes of caught adults differed in Weyher by 35% and in Pleisweiler by 67.6% between both years (Table 3.2).

Overall, we found 53 newly deposited oothecae. The number of deposited oothecae differed between 2012 and 2013 by 15.8% in Weyher, and by 80% in Pleisweiler. Oothecae hatched in spring 2013 approximately one month later than in 2012. In total, we recorded 17 assured ootheca hatchings (Table 3.2).

Overall, we estimated 116 imaginal moltings. In 2012, we determined 7.7% less imaginal moltings than in 2011 in Weyher, and even 50% less moltings in Pleisweiler. In 2011, the period of imaginal molting lasted three weeks longer than in 2012 (Table 3.2).

Table 3.2. Field results on ALHE of *M. religiosa* obtained in the study areas Weyher and Pleisweiler during 2011 to 2013. For adult *M. religiosa* the results of capture-mark-recapture experiments are listed. The recapture rates are the quotients of the respective number of recaptures and the number of first captures. For oothecae the numbers of deposition, hatching (assured by hatching remains on ootheca), and the time period of hatching are shown. The study started in mid May 2011 and thus did not monitor ootheca hatching in 2011. For this reason, ootheca hatching was checked in spring 2013. To estimate the number of imaginal moltings we used the number of newly found, unmarked imagines, which were recorded during, or one week after the last larvae record.

	Weyher			Pleisweiler		
	2011	**2012**	**2013**	**2011**	**2012**	**2013**
Adults						
no. of first captures	32 (19♂ 13♀)	48 (22♂ 26♀)	-	91 (43♂ 48♀)	32 (15♂ 17♀)	-
no. of recaptures	20 (6♂ 14♀)	32 (10♂ 22♀)	-	48 (15♂ 33♀)	13 (3♂ 10♀)	-
recapture rates	0.63 (0.32♂ 1.08♀)	0.67 (0.46♂ 0.85♀)	-	0.53 (0.35♂ 0.69♀)	0.41 (0.20♂ 0.59♀)	-
Oothecae						
no. of depositions	16	19	-	15	3	-
no. of assured hatchings	-	7	5	-	4	1
hatching period	-	17 May – 2 June	22 June – 12 July	-	26 May – 25 June	15 June
Imaginal moltings						
no. of moltings	22	19	-	56	19	-
molting period	18 July – 23 August	31 July – 13 August	-	25 July – 22 August	30 July – 7 August	-

3.4.1.2 Mapping of study sites - Environmental variables

Vegetation. In Weyher, the mean vegetation height was significantly lower in August 2011 (after mowing, 19.85 cm ± 8.32 SD, n = 42) than in August 2012 (without mowing, 28.05 cm ± 14.35 SD, n = 46; paired Wilcoxon-Test: U = -2.845, n = 42, P = 0.004). In Pleisweiler, the mean vegetation height was significantly higher in August 2011 (without grazing, 25.42 cm ± 6.10 SD, n = 78) than in August 2012 (after grazing by sheep and goats, 14.85 cm ± 6.11 SD, n = 90; paired Wilcoxon-Test: U = -6.983, n = 78, P < 0.001). We used the Wilcoxon-Test as data was not normally distributed.

Temperature and relative humidity. The marked-out study area in Weyher was slightly warmer and wetter than the area in Pleisweiler (two-years-mean). Spring (1 May – 30 June) in 2011 was the driest and for Pleisweiler likewise the warmest, whereas spring in 2013 was definitely the coldest and wettest spring at both study areas. During spring, the mean daily temperature differed in the majority of cases between the areas, and between the years (Table 3.3).

In Weyher and Pleisweiler, the daily mean temperature over the entire study time differed significantly between most of the substrates (paired Wilcoxon-Test for non-normally distributed data; Table 3.4; Online Resource 3.1). In a two-years-mean, the warmest substrate was *HS* in Weyher, followed by *WP,* and in Pleisweiler it was *BE*, followed by *HS* (Table 3.4).

Table 3.3. Mean temperatures and relative humidities ± SD during spring in 2011, 2012 and 2013, and the entire study period (2011 to 2013) for both study areas. (a) Mean temperature ± SD and mean relative humidity ± SD in Weyher and Pleisweiler; values are based on the time periods 19 May – 30 June 2011, 1 May – 30 June 2012, 1 May – 30 June 2013, and 19 May 2011 – 29 July 2013, respectively. (b) Results from two-sided paired Student's t-tests ($^{\Delta}$) and Wilcoxon-Tests ($^{\blacktriangle}$, for non-normally distributed data), respectively, on differences in temperatures and in relative humidities. For each study area differences between years are tested and sites are compared for each year and eventually for the entire study period; shown are t-values (t) or U-values (U), degrees of freedom (df) and P-values with significance levels. Significant tests are highlighted * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

(a) Raw data	**Temperature (°C) ± SD**	**Relative humidity (%) ± SD**
Weyher		
2011 (19 May – 30 June)	19.83 ± 3.49	73.07 ± 16.17
2012 (1 May – 30 June)	19.12 ± 3.74	80.09 ± 7.78
2013 (1 May – 30 June)	15.97 ± 4.33	89.76 ± 5.07
2011 – 2013	12.80 ± 8.28	86.32 ± 10.60
Pleisweiler		
2011 (19 May – 30 June)	19.83 ± 4.09	69.98 ± 13.91
2012 (1 May – 30 June)	18.16 ± 3.62	80.46 ± 9.85
2013 (1 May – 30 June)	15.33 ± 3.63	87.40 ± 4.21
2011 – 2013	11.94 ± 8.08	84.25 ± 12.09

(b) Student's t-test / Wilcoxon-Test	**t / U**	**df**	**P**	**t / U**	**df**	**P**
Weyher						
2011 vs. 2012	1.83$^{\Delta}$	42	0.074	-2.24$^{\Delta}$	42	0.030*
2011 vs. 2013	6.83$^{\Delta}$	42	<0.001***	-6.49$^{\Delta}$	42	<0.001***
2012 vs. 2013	4.07$^{\Delta}$	60	<0.001***	-7.23$^{\Delta}$	60	<0.001***
Pleisweiler						
2011 vs. 2012	2.73$^{\Delta}$	42	0.009**	-3.32$^{\Delta}$	42	0.002**
2011 vs. 2013	7.55$^{\Delta}$	42	<0.001***	-7.67$^{\Delta}$	42	<0.001***
2012 vs. 2013	4.15$^{\Delta}$	60	<0.001***	-4.67$^{\Delta}$	60	<0.001***
Weyher vs. Pleisweiler						
2011	-0.05$^{\Delta}$	42	0.960	3.48$^{\Delta}$	42	0.001***
2012	8.12$^{\Delta}$	60	<0.001***	-0.68$^{\Delta}$	60	0.498
2013	5.13$^{\Delta}$	60	<0.001***	5.67$^{\Delta}$	60	<0.001***
2011 – 2013	-19.14$^{\blacktriangle}$	801	<0.001***	-11.82$^{\blacktriangle}$	801	<0.001***

Table 3.4. Mean temperatures and relative humidities ± SD of different substrates for Weyher and Pleisweiler. Mean temperatures and mean relative humidities are based on daily mean values of the entire study period (2011-2013). (a) Mean temperature (°C) and mean relative humidity (%) ± SD for the substrates herbaceous plants (*HP*), woody plants (*WP*), hard substrates (*HS*) and blank earth (*BE*). (b) Results of paired Wilcoxon tests (U-values, df, and P-values with significance levels) for differences in temperatures and relative humidities (2011-2013) between substrates *HP*, *WP*, *HS*, and *BE* for each study area. Significant tests are highlighted * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

(a) Raw data	**Temperature (°C) ± SD**	**Relative humidity (%) ± SD**
Weyher		
HP	12.024 ± 8.246	85.798 ± 10.383
WP	12.710 ± 8.432	84.788 ± 11.530
HS	12.902 ± 7.609	82.823 ± 13.449
BE	12.692 ± 8.796	90.169 ± 10.194
Pleisweiler		
HP	11.299 ± 8.028	89.309 ± 8.552
WP	11.659 ± 8.246	83.047 ± 11.944
HS	12.491 ± 8.138	83.031 ± 14.402
BE	13.673 ± 10.929	86.076 ± 12.434

(b) Wilcoxon-Test	**U**	**df**	**P**	**U**	**df**	**P**
Weyher						
HP vs. *WP*	-0.122	740	0.903	-2.069	740	0.039*
HP vs. *BE*	-10.466	738	<0.001***	-15.486	738	<0.001***
HP vs. *HS*	-6.638	740	<0.001***	-8.071	740	<0.001***
WP vs. *BE*	-10.143	738	<0.001***	-17.545	738	<0.001***
WP vs. *HS*	-3.930	801	<0.001***	-9.212	801	<0.001***
BE vs. *HS*	-2.022	738	0.043*	-17.373	738	<0.001***
Pleisweiler						
HP vs. *WP*	-10.281	740	<0.001***	-17.001	740	<0.001***
HP vs. *BE*	-11.296	738	<0.001***	-10.327	738	<0.001***
HP vs. *HS*	-9.501	740	<0.001***	-13.968	740	<0.001***
WP vs. *BE*	-16.030	738	<0.001***	-8.900	738	<0.001***
WP vs. *HS*	-14.678	801	<0.001***	-1.308	801	0.191
BE vs. *HS*	-3.864	738	<0.001***	-7.817	738	<0.001***

3.4.2 Habitat requirements for adult roosting and life history events

3.4.2.1 Modelling habitat preference of imagines

As Stärz et al. (2010) observed differences in habitat usage of sexes, we separately analyzed habitat preference of female and male *M. religiosa*. Overall, we captured females 1.38 times more often than males.

Males. For males the chi^2-goodness of fit tests suggested an unproportional usage of substrates compared to substrate availability in Weyher in both study years (2011: $\chi^2 = 85.73$, df = 2, $P < 0.001$; 2012: $\chi^2 = 198.55$, df = 2, $P < 0.001$). In Pleisweiler, no preference for any substrate could be detected. Males used substrates proportional to substrate availability in both years (2011: $\chi^2 = 4.91$, df = 2, $P = 0.086$; 2012: $\chi^2 = 2.04$, df = 2, $P = 0.362$).

The HPI revealed that male *M. religiosa* preferred *WP* as roosting habitat in Weyher (Fig. 3.2). *HS* was only used in 2011, whereas it was strictly avoided in 2012. In both years males strictly avoided *BE.* In Pleisweiler, males most frequently used *HP* in both years, which was the most frequent substrate, and is consistent with a use of substrates proportional to substrate availability. Males did not use *HS* and *BE* in any of the two years.

The best logistic regression models tested for male presence in grid cells were *day* + *mean veg height* + *loc* (AIC = 1388.8, $R^2_N = 0.055$) and *day* + *mean veg height* (AIC = 1392.4, $R^2_N = 0.051$). They indicate that vegetation height seems to be important for males. A number of other models were even worse in terms of AIC and R^2_N (Table 3.5) than these two models.

Females. For females the chi^2-goodness of fit tests indicated an unproportional usage of substrates compared to substrate availability in Weyher in 2011 and 2012 (2011: $\chi^2 = 77.12$, df = 2, $P < 0.001$; 2012: $\chi^2 = 174.88$, df = 2, $P < 0.001$). For females in Pleisweiler the chi^2-goodness of fit tests showed only in 2011 an unproportional usage of substrates, but not for 2012 (2011: $\chi^2 = 9.14$, df = 2, $P = 0.010$; 2012: $\chi^2 = 1.02$, df = 2, $P = 0.599$). The HPI revealed that in Weyher females always preferred *WP* as roosting habitat. In 2012, *HS* was less often used by females than in 2011. *BE* was strictly avoided by females in both years. In Pleisweiler, females most frequently used the most common substrate *HP* in 2011 and 2012. *HS* and *BE* were less frequently used in 2011 than in 2012. In 2012, no female was found on *BE* (Fig. 3.2).

The best logistic regression models identified for female roosting in grid cells were *day* + *mean veg height* + *loc* (AIC = 1807.8, $R^2_N = 0.020$) and *day* + *mean veg height* (AIC = 1811.3, $R^2_N = 0.016$). A number of other models were worse in terms of AIC and R^2_N (Table 3.5) than these two models.

3.4.2.2 Modelling habitat preference for ootheca deposition

Female *M. religiosa* deposited ootheca on substrates unproportional to their availability in the areas, except for Pleisweiler in 2012 (chi^2-goodness of fit test; Weyher: 2011: $\chi^2 = 14.29$, df = 2, P = 0.001; 2012: $\chi^2 = 33.97$, df = 2, P < 0.001; Pleisweiler: 2011: $\chi^2 = 37.55$, df = 2, P < 0.001; 2012: not calculated due to a too small sample size).

For both sites the HPI indicates that females preferred *HS* for ootheca deposition in both years (Fig. 3.2). *WP* was the second most preferred substrate for ootheca deposition in 2011 at both sites, and in 2012 only in Weyher. In Pleisweiler, no ootheca was deposited on *WP* in 2012. The substrate *BE* was never used for ootheca deposition at neither study site and in neither year.

Ootheca deposition was best described by the logistic regression model $temp + temp^2 + day + day^2$ (AIC = 132.090, $R^2_N = 0.089$). Other regression models were less statistically supported in terms of AIC and R^2_N (Table 3.5).

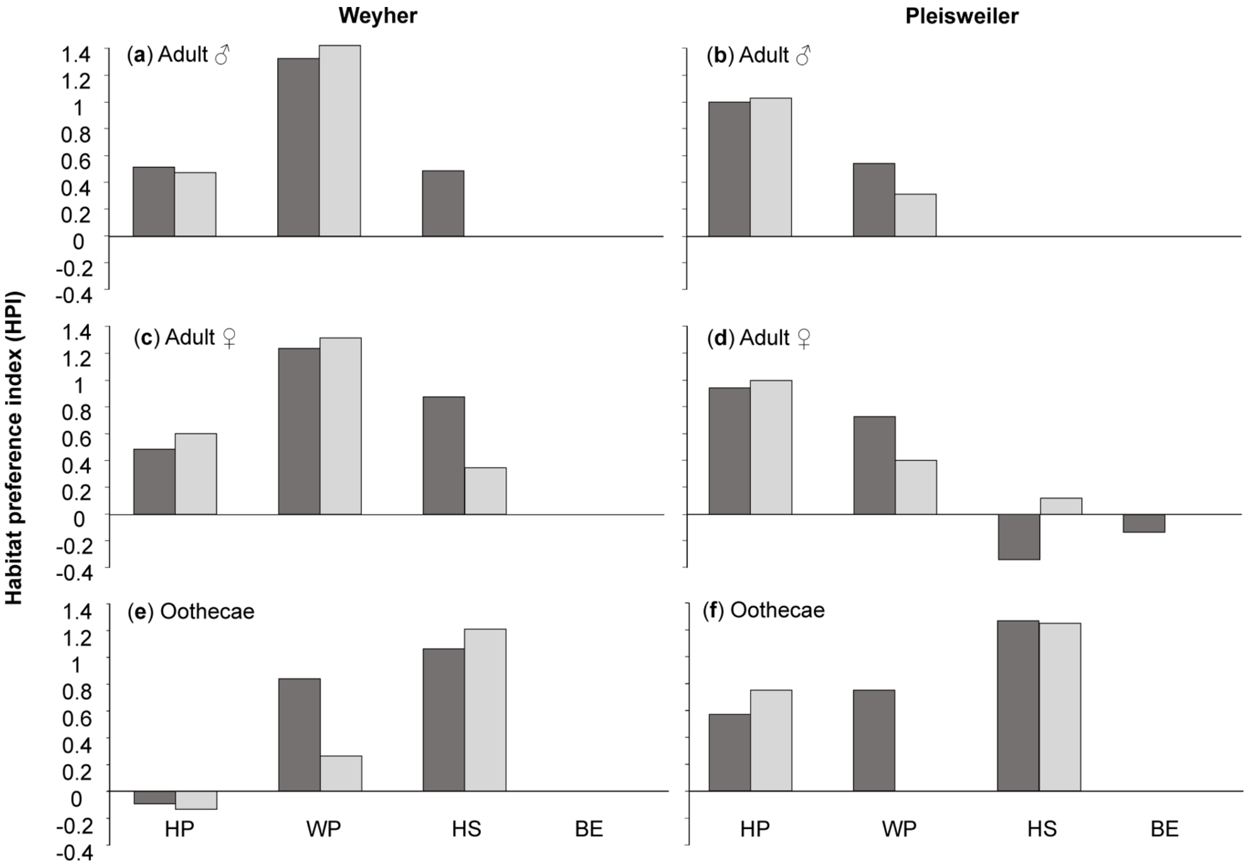


Fig. 3.2. Habitat preference index (HPI, Lille 1996) for (a, b) male (♂), (c, d) female (♀) and (e, f) oothecae deposition of *M. religiosa* and each study area. Dark grey bars represent 2011, and light grey bars 2012. In 2011, 47.7% of the study area Weyher was *HP*, 23.5% was *WP*, 28.3% was *HS*, and 0.5% was *BE*. In 2012, 42.3% of the study area Weyher was *HP*, 27.4% was *WP*, 28.3% was *HS*, and 2% was *BE*. In 2011, 80.9% of the study area Pleisweiler was *HP*, 8.9% was *WP*, 7.4% was *HS*, and 2.8% was *BE*. In 2012, 79.7% of the study area Pleisweiler was *HP*, 7.6% was *WP*, 8% was *HS*, and 4.7% was *BE.*

3.4.2.3 Modelling ootheca hatching

The best logistic regression models describing the microhabitat conditions needed for ootheca hatching were univariate. One model consisted of the variable *temp*, and was statistically well supported (AIC = 79.418; R^2_N = 0.311). The probability of ootheca hatching follows a saturation curve with increasing previous week mean temperatures. This curve predicts a saturation probability of one at a temperature of about 27°C. The second model consisted of the predictor variable *substr*, but it was much less statistically supported than the best model (Table 3.5).

Table 3.5. Logistic regression models for presence of adult males and females, ootheca deposition, and ootheca hatching in grid cells. Field data on each ALHE were pooled from both study areas and from the entire study period to establish models. Shown are the five best models for each ALHE (for ootheca hatching we only found two significant models). Selection of models was based on a significant difference from the null model, AIC (Akaike information criterion; ΔAIC approach, Burnham & Anderson 2004) and Nagelkerke's R^2 (R^2_N) values. All models listed were neither subject to model over nor under dispersion. AIC values with degrees of freedom (df_{AIC}), R^2_N with degrees of freedom ($df_{R^2_N}$), values of estimated regression coefficients (*β* values) with SE, and the estimated intercept with SE. Significant predictor variables are highlighted ° $P < 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Models	**AIC**	**df_{AIC}**	**R^2_N**	**$df_{R^2_N}$**	***β1* ± SE**	***β2* ± SE**	***β3* ± SE**	***β4* ± SE**	**Intercept ± SE**
Male presence									
β1 day+ β2 mean veg height+ β3 loc	1388.8	12161	0.055	12165	-0.233 ± 0.033***	0.025± 0.007***	0.442 ± 0.184*		-4.574 ± 0.306***
β1 day+ β2 mean veg height	1392.4	12162	0.051	12165	-0.230 ± 0.033***	0.029± 0.007***			-4.079 ± 0.218***
β1 mean veg height	1449.4	12163	0.008	12165	0.026 ± 0.007***				-5.103 ± 0.189***
β1 day	1482.0	12953	0.035	12955	-0.206 ± 0.031***				-3.527 ± 0.152***
β1 loc	1525.3	12953	0.005	12955	0.459 ± 0.173**				-5.162 ± 0.261***
Female presence									
β1 day+ β2 mean veg height+ β3 loc	1807.8	12204	0.020	12208	-0.098 ± 0.025***	0.022± 0.006***	0.378 ± 0.159*		-4.723 ± 0.272***
β1 day+ β2 mean veg height	1811.3	12205	0.016	12208	-0.095 ± 0.025***	0.025± 0.006***			-4.299 ± 0.199***
β1 mean veg height	1824.9	12206	0.007	12208	0.024 ± 0.006***				-4.774 ± 0.168***
β1 max veg height	1832.9	12206	0.003	12208	0.006 ± 0.003*				-4.553 ± 0.174***
β1 min veg height	1833.1	12206	0.003	12208	-0.129 ± 0.074°				-4.127 ± 0.093***
Ootheca deposition									
β1 temp+ β2 temp^2*+ β3 day + β4 day*^{2}	132.1	368	0.089	373	-0.728 ± 0.307*	0.019± 0.008*	0.690 ± 0.384°	-0.001 ± 0.001°	-80.90 ± 40.868°
β1 max height	766.7	13265	0.021	13267	0.008 ± 0.002***				-6.195 ± 0.266***
β1 day + β2 year	995.5	14061	0.058	14064	0.034 ± 0.005***	-0.828± 0.228***			1652 ±459.200***
β1 day + β2 day^2	1000.2	14061	0.053	14064	0.419 ± 0.143**	-0.001± 0.0003**			-60.428 ± 10.887***
β1 day	1007.4	14062	0.044	14064	0.032 ± 0.005***				-13.477 ± 1.360***
Ootheca hatching									
β1 temp	79.4	138	0.311	140	0.499 ± 0.123***				-10.867 ± 2.330***
β1 substr	166.1	409	0.027	411	-0.737 ± 0.435°				-1.179 ± 1.002

3.4.3 Effect of conservation measure on temperature

Conservation measures caused an increase in temperature during warm months, compared to temperatures expected without conservation measures on the substrate *HP* (chi^2-goodness of fit, H_0 = deviations are random; Weyher: $\chi^2 = 6.89$, df = 1, P = 0.009; Pleisweiler: $\chi^2 = 18.00$, df = 1, P < 0.001). The residual temperatures (observed - expected temperature) were significantly higher in Pleisweiler (3.09°C ± 2.34 SD) than in Weyher (2.72°C ± 2.19 SD; Mann-Whitney U-test: U = -2.069, n = 493, P = 0.039; Fig. 3.3).

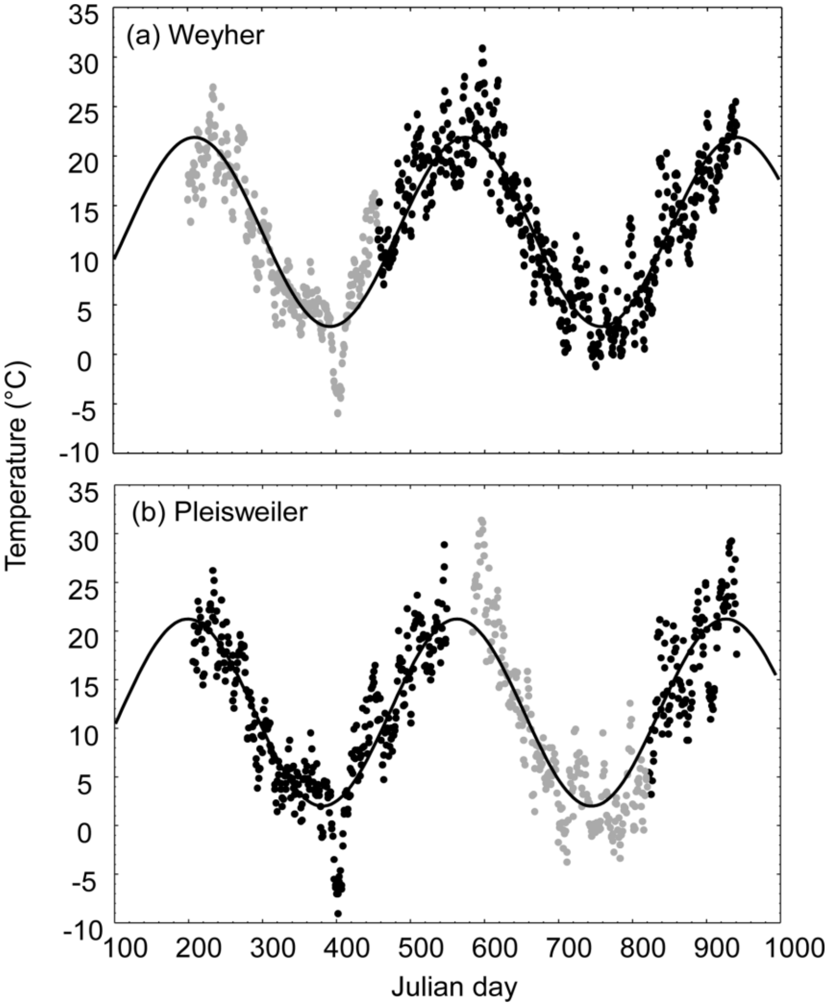


Fig. 3.3. Daily mean temperatures on *HP* with (grey dots) and without (black dots) the time period influenced by conservation measures in (a) Weyher and (b) Pleisweiler. For each study site daily mean temperatures are calculated from a single data logger, which was installed on *HP* and was left unchanged on the same position during the complete study site. The curves in (a) and (b) result from fitting respective temperatures values marked by black dots to formula 1 (Weyher: y = 9.545*(sin(2*π*(x-117.088)/365)+1)+2.792; $SE_{residual}$ = 3.289, df = 483; Pleisweiler: y = 9.694*(sin(2*π*(x-106.911)/365)+1)+1.833; $SE_{residual}$ = 3.677, df = 462). In Weyher and Pleisweiler conservation measures induced lower temperatures in colder months than without the measure, and in Pleisweiler they caused higher temperatures in warmer months.

3.5 Discussion

Stärz et al. (2010) already showed that life stages of *M. religiosa* used different vegetation structures. Our study corroborates these authors. Differences in microhabitat use within the life cycle have also been found for various other insect species (Joern 1982; Kemp et al. 1990; Fartmann 1997). However, for planning and implementation of conservation measures for populations such information is essential.

Temperature and relative humidity correlated over the entire study period at both study sites. This precludes the disentangling of the influence of any of the two variables on ALHE of *M. religiosa*. We therefore only concentrated on the effect of temperature on ALHE as temperature predominantly affects insects (Beck 1983).

Most of our best logistic regression models on ALHE repeatedly suggested a considerable influence of the control variables *day* and *loc* on presence. Thus, these models mainly capture the expected phenology of *M. religiosa* over the year (*day*) and the overall differences in microclimatic conditions between sites (*loc*), whereas significant additional predictor capture the variability in microclimatic conditions between years and sites.

Our logistic regression models on ALHE were developed based on the environmental conditions in our two marked-out study areas, under which *M. religiosa* was able to establish stable populations. As these conditions only comprise a small subset of the temperature range and structures under which the species is able to survive, the application of our models for ALHE to other geographic regions is limited because of the risk of model extrapolation.

3.5.1 Habitat preference of adults

The HPI indicated that males generally avoided *HS*, whereas females used this substrate for ootheca deposition. As both sexes were never observed on *BE* of neither study site, this could indicate that adults generally avoid substrates on which they are exposed to predators. Males and females preferred *WP* as roosting substrate in Weyher, whereas in Pleisweiler they predominantly used the most frequent substrate *HP*. In Weyher, *WP* mainly consisted of the plant genera *Genista* (flowering time: April – June), *Rubus* (May – August), and *Solidago* (July – September; Fitter et al. 1974). The flowering time of these genera, in which they attract numerous insects including potential prey species of *M. religiosa*, strongly overlaps with the adult phase of *M. religiosa*. In Pleisweiler, the majority of plants flowering during the adult phase were found on the substrate *HP*. The genus *Prunus* was in Pleisweiler the dominating flowering species in *WP*, which flowers between March and May (Fitter et al. 1974). James (1958) and Berg et al. (2011) corroborate our result that microhabitat selection of roosting adults depends on prey availability.

Irrespective of their low statistical support, the best logistic regression models consistently predicted a positive effect of the mean vegetation height on adult presence in grid cells. Habitats with higher vegetation offer suitable hiding places for the camouflaged *M. religiosa* and give this species shelter from predation. They also enable prey ambushing and thus guarantee good nourishment conditions for *M. religiosa* (Schmidt & Bühl 1970; Joern 1982; Gottschalk et al. 2003). Stärz et al. (2010) also observed that adult *M. religiosa* favoured higher-growing vegetation for roosting. However, maximum vegetation height measured within grid cells was not included as predictor in any of the models on adult presence (Table 3.5). As *M. religiosa* usually inhabits open habitats (Berg et al. 2011), we conclude that the optimal vegetation height for roosting adults is larger than the mean and lower than the maximum vegetation height measured in grid cells.

Although *M. religiosa* is thermophilic, an expected effect of temperature on the presence of adult *M. religiosa* in grid cells was only indirectly supported in our models by the significant control variable *day*.

3.5.2 Ootheca deposition

Our results corroborate that *M. religiosa* has climatic and structural preferences for timing of ootheca deposition and for choosing deposition places (Ingrisch & Boekholt 1982; Eisenberg & Hurd 1990).

Although we frequently found ootheca attached to *HP*, as known from literature (Schoppmann & Schoppmann 1988; Stärz et al. 2010), the HPI indicated a strong preference for *HS* for ootheca deposition by females. In our study areas, *HS* mostly comprises stone walls with niches and protruding stones. This substrate was due to its good heat storage capacity in a two-years-mean the warmest and driest substrate in Weyher, and it was the second warmest substrate in Pleisweiler. In summer, *HS* was one of the coldest substrates in Weyher, whereas in winter it was always the warmest substrate (Online Resource 3.1). In Weyher, the second warmest substrate *WP* was also frequently used for ootheca deposition in 2011 (Ehrmann 1985; Hevers & Liske 1991; Berg et al. 2011). *HP* having the lowest two-years-mean temperature in both study sites, was only slightly avoided for ootheca deposition in Weyher in both years. In Pleisweiler, *HP* was as frequently used for ootheca deposition in 2011 and 2012 as *WP* in 2011. Differences observed in the choice of substrates for ootheca deposition by females between Weyher and Pleisweiler could possibly result from the unequal sizes of the marked-out areas studied and the resulting differences in the reachability of *HS* by females. The study area in Weyher was narrow and the straight-line distance for females to travel from roosting places to *HS* was maximal 3 m, whereas in Pleisweiler the maximal distance was 11 m (Fig. 3.1). However, the radius of movement of a female *M. religiosa* during its complete imaginal period only ranges up to 30 m (Ehrmann 1985; Hideg 1994; Stärz et al. 2010). Berg et al. (2011) also observed that *HP* can replace *HS* for ootheca deposition, if *HS* is absent or not reachable.

In both study areas, we did not find any ootheca on the substrate *BE*. Extreme hot and dry conditions during summer as well as missing structures for ootheca fixation and their exposition to predators presumably explain the absence of ootheca on *BE* (Ehrmann 1985; Detzel & Ehrmann 1998). Exposition to predators and weather could also explain the absence of ootheca on *WP* as observed in Pleisweiler in 2012: after grazing by sheep and goats, *WP* were defoliated (personal observation) and shrub trunks did not provide shelter and cover for ootheca.

The logistic regression model indicated an effect of time (*day*) and temperature (*temp*) on ootheca deposition. The probability of ootheca deposition decreased towards the end of the year and with declining temperatures.

3.5.3 Ootheca hatching

In both study areas, the spring in 2013 was significantly colder and wetter than in 2012. This resulted in a delay in ootheca hatching of approximately one month in 2013 compared to 2012. Other authors corroborate that cold and wet springs can delay ootheca hatching and can sometimes even drive *M. religiosa* populations to extinction (Ehrmann 2003; Liana 2007; Stärz et al. 2010).

Our logistic regression model supports an effect of temperature on ootheca hatching (*temp*; $R^2_N = 0.311$). This model predicts for mean temperatures of the previous week (ca. 17°C up to 27°C) that the probability of ootheca hatching increases exponentially with increasing temperatures. This temperature range is consistent with observations of other authors. James (1958) reports 19°C to 26°C for egg hatching in *M. religiosa*, and Przibram (1907) reports a minimum temperature of 17°C for the postembryonic development of *M. religiosa*. Hideg (1991) defined the optimal temperature for *M. religiosa* between 25°C and 30°C. High temperature thresholds for ootheca hatching most likely diminish the risk of larvae dying during late spring frosts. The thresholds also assure warm and dry conditions during larval development (Ehrmann 2003; Liana 2007; Berg et al. 2011), and guarantee a sufficient food availability for larvae after hatching from ootheca as the development of arthropods, the common prey of *M. religiosa* is also accelerated by such climatic conditions (Ingrisch 1978; Ratte 1985).

3.5.4 Imaginal molting

Under warm Mediterranean temperatures as seen in Spain adult *M. religiosa* emerge in May (Kaltenbach 1962 in Ingrisch 1978), whereas in the colder Germany, at the border of its northern distribution area, larval development is typically completed in late July or August. Analogously, we observed in total 48% more imaginal moltings and a 57% longer period of imaginal molting on both study sites in the warmer year 2011 than in the colder year 2012. The spring in 2011 was the driest and partly the warmest of all three years on both study areas. Consequently, more *M. religiosa* larvae survived in 2011 than in 2012 as cold and wet springs inhibit development and growth of larvae (Hideg 1991) and also provoke food shortage (Ingrisch 1978; Ratte 1985). Unfortunately, our sample on imaginal molting was insufficient to conduct any reliable statistical analyses on environmental conditions effecting larval development.

3.5.5 Conservation measures

The areas inhabited by the two *M. religiosa* populations were subject to conservation measures during the larval phase. Contrary to our expectations, these measures considerably reduced adult population sizes (Table 3.2) and the reproduction rate of the populations (ootheca deposition), compared to sizes and rates observed in the years without such interventions. Also Stärz et al. (2010) noticed a decrease in the size of *M. religiosa* populations in southern Germany after conservation measures took place in winter. In Pleisweiler, the negative effect of measures on adult population size and reproduction rate was stronger than in Weyher. This difference might have been strengthened by differences in spring temperatures and humidities between 2011 and 2012.

In Pleisweiler, grazing caused a strongly diminished and stamped down vegetation with isolated small tufts of grass. This considerably increased ambient temperature in warm periods and decreased temperatures in cold periods (Fig. 3.3). Grazing and mowing in July and August causes high sward temperatures due to the absence of shady vegetation. It forces grasshoppers (Stärz et al. 2010) and other prey of *M. religiosa* to leave the treated sites in order to avoid overheating (Gardiner & Hassall 2009).

In Weyher, the vegetation was cut to 30 cm with a clearing saw in June/ July 2011, which induced a much slighter temperature change than grazing in Pleisweiler (Mann-Whitney U-test; Fig. 3.3). This method is also gentler regarding the ground fauna (Humbert et al. 2009) and permits the development of potential prey populations for *M. religiosa*.

Humbert et al. (2009) and Stärz et al. (2010) advise tending strategies for areas inhabited by *M. religiosa* which result in a mosaic of long and short vegetation, as these conserve habitat diversity. *Mantis religiosa* especially benefits from changing grazing sites, where uncut grass strips are fenced-off from grazing, giving shelter to *M. religiosa* as well as to their prey (Cungs 2003 summarized in Berg et al. 2011). We recommend this strategy for Pleisweiler. Limiting grazing by sheep and goats to smaller fenced areas and shortening the grazing duration will still force grazers to browse on shrubs after weeds are reduced but will also preserve the ground fauna.

For ootheca deposition *M. religiosa* prefers sheltering and heat storing substrates as such conditions accelerate egg development. Late ootheca hatching, resulting from low temperatures during egg development, can even prevent *M. religiosa* to reach the adult stage and hence prevent reproduction within the vegetation period. This phenomenon is repeatedly observed in *M. religiosa* populations located at the edge of the distribution range (Liana 2007). To improve the present situation for *M. religiosa* populations in Germany, conservation measures should emphasize more on the conservation of heat storing structures such as hard substrates in habitats. Hence, even anthropogenic structures such as barracks in former military training areas or dry stone walls in former vineyards should not be removed completely.

3.6 Acknowledgements

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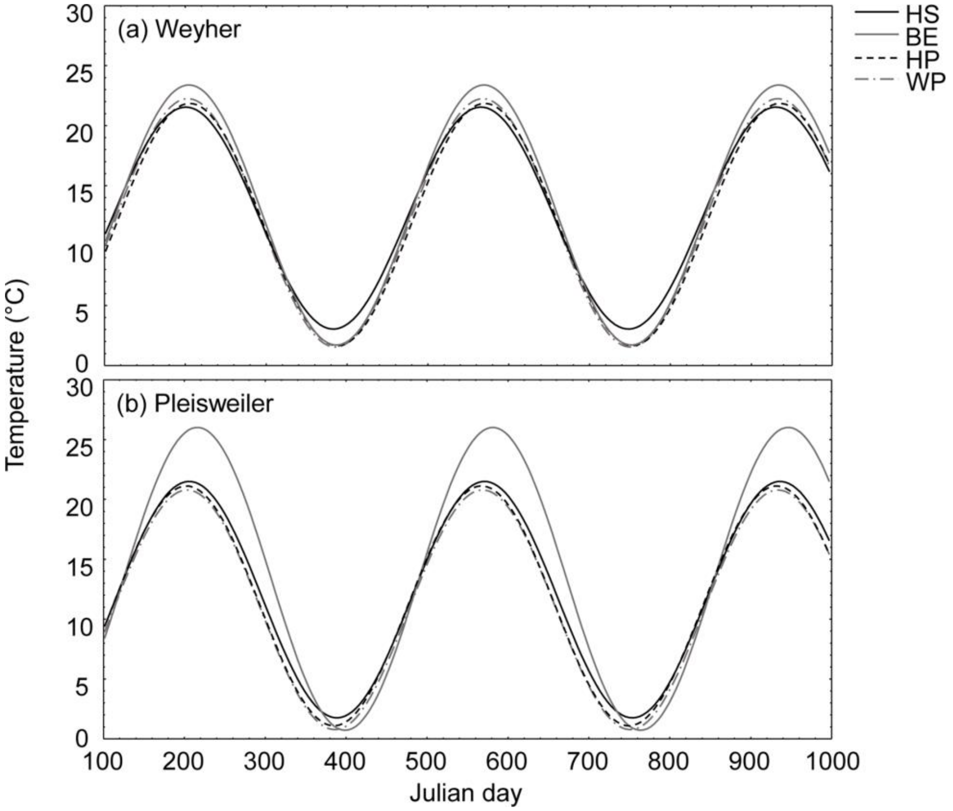
Sample notification: The capture and handling of *M. religiosa* was approved by the Struktur- und Genehmigungsdirektion Süd von Rheinland-Pfalz, Permit #42/553-254.

3.7 Supplementary material

3.7.1 Annual temperature regimes on substrates



Online Resource 3.1. Annual temperature regimes on substrates *BE* (grey solid line), *HP* (black dashed line), *HS* (black solid line), and *WP* (grey dash-dotted line) for (a) Weyher and (b) Pleisweiler. For each study site and substrate daily mean temperatures are averages over all data loggers installed on the substrate. The curves in (a) and (b) result from fitting respective temperature values from the entire study period to formula 1.

Fitted functions for Weyher:
BE y = 10.879*(sin(2*π*(x-111.897)/365)+1)+1.666 ($SE_{residual}$ = 4.171, df = 737);
HP y = 10.136*(sin(2*π*(x-113.005)/365)+1)+1.724 ($SE_{residual}$ = 3.974, df = 739);
HS y = 9.291*(sin(2*π*(x-108.105)/365)+1)+2.889 ($SE_{residual}$ = 3.639, df = 800);
WP y = 10.397*(sin(2*π*(x-110.711)/365)+1)+1.523 ($SE_{residual}$ = 3.926, df = 800).

Fitted functions for Pleisweiler:
BE $y = 12.737*(\sin(2*\pi*(x-123.514)/365)+1)+0.767$ ($SE_{residual} = 6.109$, df = 737);
HP $y = 10.081*(\sin(2*\pi*(x-108.709)/365)+1)+1.056$ ($SE_{residual} = 3.58$, df = 739);
HS $y = 9.949*(\sin(2*\pi*(x-113.357)/365)+1)+1.802$ ($SE_{residual} = 3.932$, df = 800);
WP $y = 10.082*(\sin(2*\pi*(x-110.893)/365)+1)+0.811$ ($SE_{residual} = 3.956$, df = 800).

3.7.2 Modelling with MaxEnt

In logistic regression analysis pseudo-absences could be problematic, as the absence of an ALHE (roosting Adults and the three Life-History Events egg deposition, egg hatching, and imaginal moulting) of *M. religiosa* in a grid cell does not necessarily indicate the absence of the species in this cell. In order to minimize the error introduced by pseudo-absences, I additionally used for all ALHE the Maximum Entropy modelling approach (MaxEnt) as implemented in the software MaxEnt (version 3.3.3k; Phillips et al. 2004), using presence-only data.

3.7.2.1 Material and Methods

To increase the datasets on ALHE for MaxEnt modelling, I pooled the data obtained on adult presence and life history events of both study areas within 2011 and 2012 into one large dataset. However, for imaginal moulting I was unable to establish a reliable model, because the data set on moulting was too small. For each ALHE of *M. religiosa* I considered the same environmental predictor variables and an analogous modelling procedure as used in the logistic regression analyses (Table 3.1). I further tested the current ambient temperature close to the individual or ootheca (predictor variable $temp_{ind}$; measured with digital thermometer GTH 175/MOP, ± 0.2°C, Greisinger electronics). As for none of the ALHE any univariate model was sufficiently supported in terms of significant deviation from the null model (except of one model, Online Resource 3.3), I had to change my approach to establish multivariate models. Instead of combining the variables of the best supported univariate models into one single multivariate model as was done in the logistic regression analysis (forward testing, Kennedy & Bancroft 1971) I started in MaxEnt with a model consisting of all (non-correlated) environmental variables as potential predictors. I then stepwise excluded those variables that contributed less than 1% to the variation explained by the model (sequential deletion), until I found the final model with the highest AUC (area under receiver operating characteristic curve) and AUC_{tested} (AUC_{tested} is the AUC value observed for the internal validation dataset, see below). As I predominantly focused on habitat conditions enabling the presence (and not so much the absence) of *M. religiosa* under specific microclimatic conditions, I used the maximum training sensitivity and specificity as well as the maximum test sensitivity and specificity to rate quality of models. For the internal evaluation of models, I used besides the AUC also the proportion of training omission rate and of test omission rate to fractional predicted area of the maximum training sensitivity plus specificity and of the maximum test sensitivity plus specificity, but also took into consideration the logistic threshold assumed for these proportions. All values used for model validation are given in the MaxEnt output.

In order to validate the models calculated by MaxEnt, I first ran an internal validation with random test percentages of our datasets as implemented in this software. I tested several random test percentages by running test models with various test percentages (10%, 15%, 20%, 25%, 30%, and 35%) to identify the best test percentage for each data set (datasets: adult presence, egg deposition, ootheca hatching). The best test percentage was chosen by identifying the settings of the model with the lowest test percentage and the highest $\mathrm{AUC}_{\mathrm{tested}}$-values. Next, the best regularization multiplier for controlling model over- or under fitting was identified by choosing the settings of the model with the highest AUC and $\mathrm{AUC}_{\mathrm{tested}}$ values after testing multipliers of 0.01, 0.1, 1, and 3 according to Phillips et al. (2004). For each dataset, the best random test percentage for internal model validation was 20% and the best regularization multiplier was equal to 1. Using these two settings I ran models, excluding over- or under fitting right at the outset. I used the standard settings of the software where training stopped after reaching a maximum of 500 iterations of the optimization algorithm.

3.7.2.2 Results

The best multivariate model for male presence in terms of AUC derived from the MaxEnt approach (for univariate models refer to Online Resource 3.3) consisted of the predictor variables *day* (67% model contribution), *year* (22.3% model contribution), *loc* (9.3% model contribution), and *max veg height* (1.4% model contribution; Online Resource 3.2). It had a high AUC of 0.805 and $\mathrm{AUC}_{\mathrm{tested}}$ of 0.742, but the low logistic threshold assumed for AUCs suggests a lower model quality (a high threshold is needed for a sufficient discrimination of presences and absences in the internal validation). More variables did not improve the logistic threshold of the model. Nevertheless, the model corroborates that vegetation height has a slight effect on the presence of males; the probability of male presence in grid cells increases slightly with an increasing vegetation height. Temperature did not have any direct effect on the presence of males.

The best multivariate model for female presence in terms of AUC derived from the MaxEnt approach (for univariate models refer to Online Resource 3.3) consisted of the predictor variables *year* (68.2% model contribution), *day* (19.7% model contribution), *min veg height* (12.1% model contribution), and $temp_{(ind)}$ (0.1% model contribution). It was supported by a low AUC of 0.676 and AUC_{tested} of 0.679 (Online Resource 3.2). More variables improved the AUC, but negatively affected (decreased) the logistic threshold. Based on the relatively high logistic threshold and the low omission rate of the fractional predicted area (Online Resource 3.2), this model, nevertheless, describes rather well the presence of female *M. religiosa* in our study areas. The response curve on *min veg height* recorded close to the female indicates a negative effect of rising *min veg height* on the presence of female *M. religiosa*. $Temp_{(ind)}$ is nearly irrelevant for presence of females in grid cells.

The best multivariate model for ootheca deposition obtained from the MaxEnt approach was composed of the variables *day* (60.5% model contribution), and *substr* (39.5% model contribution) and had an AUC of 0.704 and AUC_{tested} of 0.584 (Online Resource 3.2). However, this model did not significantly differ from a random model.

The best multivariate model derived for ootheca hatching from MaxEnt (for univariate models refer to Online Resource 3.3) consisted of the variables $day_{(hatch)}$ (37.2% model contribution), $day_{(depos)}$ (35.6% model contribution), *year* (27.1% model contribution), and *temp* (<0.1% model contribution) and had an AUC of 0.965 and AUC_{tested} of 0.862 (Online Resource 3.2). The effect of temperature on ootheca hatching found in the best multivariate model was too small to reflect a reliable response curve.

Online Resource 3.2. Best multivariate models with variables affecting habitat preference of male and female *M. religiosa*, for ootheca deposition, and ootheca hatching, created with MaxEnt. Field data were pooled from both study sites and the entire study period. As I conducted back-ward testing, I only depict here the best supported model in terms of highest AUC with least parameters and highest logistic threshold. For internal model validation a random test proportion of 20% of presences was used. Shown are percent contribution of the variable to the final model, the permutation importance of the variable, the AUC and $\text{AUC}_{\text{tested}}$ (internal validation), the logistic threshold (log. thr.), fractional predicted area (FPA), training omission rate (trOR), test omission rate (teOR) and P-values with significance levels, for the maximum training sensitivity plus specificity and the maximum test sensitivity plus specificity, respectively. Significances are highlighted ° $P < 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

					Maximum training sensitivity plus specificity					**Maximum test sensitivity plus specificity**				
Models	**Percent contribution**	**Permutation importance**	**AUC**	**$\text{AUC}_{\text{tested}}$**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**
Males			0.805	0.742	0.276	0.522	0.000	0.091	0.008**	0.310	0.456	0.091	0.091	0.003**
day	67	70.7												
year	22.3	21.8												
loc	9.3	2.7												
max veg height	1.4	4.7												
Females			0.676	0.679	0.532	0.438	0.271	0.182	0.012*	0.471	0.545	0.188	0.000	0.001***
year	68.2	74.2												
day	19.7	20.4												
min veg height	12.1	5.4												
$temp_{(ind)}$	0.1	<0.1												
Ootheca deposition			0.704	0.584	0.425	0.488	0.143	0.286	0.208	0.425	0.488	0.143	0.286	0.208
day	60.5	47.5												
substr	39.5	52.5												
Ootheca hatching			0.965	0.862	0.445	0.127	0.000	0.000	0.016*	0.445	0.127	0.000	0.000	0.016*
$day_{(hatch)}$	37.2	62.7												
$day_{(depos)}$	35.6	35.3												
year	27.1	2.0												
temp	<0.1	<0.1												

Online Resource 3.3. Best univariate models with variables affecting habitat preference of male and female *M. religiosa*, for ootheca deposition, and ootheca hatching, created with MaxEnt. Field data were pooled from both study sites and the entire study period. For internal model validation a random test proportion of 20% of presences was used. Shown are the AUC and AUC_{tested} (internal validation), the logistic threshold (log. thr.), fractional predicted area (FPA), training omission rate (trOR), test omission rate (teOR) and P-values with significance levels, for the maximum training sensitivity plus specificity and the maximum test sensitivity plus specificity, respectively. The effect of the previous week temperature (*temp*) in modelling male presence were not calculable in MaxEnt due to insufficient data. Significances are highlighted ° P < 0.1; * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

			Maximum training sensitivity plus specificity					**Maximum test sensitivity plus specificity**				
Models	**AUC**	**AUC_{tested}**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**
Males												
day	0.764	0.723	0.576	0.290	0.289	0.455	0.067°	0.295	0.580	0.044	0.000	0.003**
mean veg height	0.558	0.469	0.497	0.733	0.136	0.364	0.856	0.509	0.535	0.386	0.364	0.357
substr	0.550	0.562	0.526	0.617	0.289	0.273	0.338	0.526	0.617	0.289	0.273	0.338
max veg height	0.550	0.510	0.502	0.578	0.273	0.364	0.474	0.514	0.117	0.864	0.727	0.129
year	0.535	0.451	0.521	0.553	0.378	0.545	0.831	0.468	1.000	0.000	0.000	1.000
$temp_{(ind)}$	0.531	0.618	0.496	0.736	0.156	0.091	0.169	0.513	0.657	0.311	0.091	0.066°
loc	0.528	0.525	0.513	0.677	0.267	0.273	0.502	0.513	0.677	0.267	0.273	0.502
min veg height	0.496	0.467	0.500	0.942	0.045	0.000	0.521	0.500	0.942	0.045	0.000	0.521
temp	-	-	-	-	-	-	-	-	-	-	-	-
Females												
day	0.718	0.529	0.463	0.290	0.385	0.692	0.549	0.621	0.193	0.500	0.692	0.232
temp	0.655	0.928	0.590	0.055	0.625	1.000	1.000	0.585	0.072	0.625	0.000	0.072°
$temp_{(ind)}$	0.580	0.597	0.526	0.094	0.731	0.923	0.724	0.497	0.660	0.288	0.077	0.034*
max veg height	0.575	0.473	0.520	0.103	0.688	0.818	0.315	0.473	0.404	0.562	0.455	0.255
loc	0.560	0.492	0.563	0.323	0.558	0.692	0.648	0.454	1.000	0.000	0.000	1.000
mean veg height	0.558	0.575	0.483	0.622	0.271	0.273	0.351	0.491	0.493	0.479	0.273	0.105
substr	0.551	0.505	0.536	0.332	0.596	0.692	0.675	0.482	0.950	0.000	0.000	0.510
min veg height	0.546	0.503	0.507	0.563	0.354	0.455	0.665	0.492	0.946	0.021	0.000	0.543
year	0.536	0.469	0.527	0.447	0.481	0.615	0.766	0.473	1.000	0.000	0.000	1.000

- continued on next page -

- Online Resource 3.3 continued from previous page -

			Maximum training sensitivity plus specificity					Maximum test sensitivity plus specificity				
Models	**AUC**	**AUC$_{tested}$**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**	**log. thr.**	**FPA**	**trOR**	**teOR**	**P-value**
Ootheca deposition												
day	0.730	0.663	0.462	0.426	0.214	0.143	0.026*	0.462	0.426	0.214	0.241	0.026*
mean veg height	0.686	0.601	0.511	0.324	0.333	0.500	0.302	0.478	0.368	0.333	0.333	0.138
year	0.663	0.610	0.570	0.495	0.179	0.286	0.217	0.570	0.495	0.179	0.286	0.218
temp$_{(ind)}$	0.605	0.451	0.496	0.467	0.286	0.667	0.856	0.421	0.840	0.071	0.000	0.351
substr	0.560	0.657	0.503	0.505	0.393	0.143	0.066°	0.503	0.505	0.393	0.143	0.066°
max height	0.546	0.721	0.503	0.501	0.375	0.167	0.109	0.487	0.617	0.333	0.000	0.055°
loc	0.546	0.332	0.543	0.337	0.571	1.000	1.000	0.470	1.000	0.000	0.000	1.000
min height	0.545	0.505	0.693	0.012	0.917	1.000	1.000	0.493	0.615	0.333	0.333	0.576
temp	0.500	0.500	0.500	1.000	0.000	0.000	1.000	0.500	1.000	0.000	0.000	1.000
Ootheca hatching												
day$_{(depos)}$	0.957	0.352	0.784	0.024	0.222	1.000	1.000	0.126	1.000	0.000	0.000	1.000
day$_{(hatch)}$	0.854	0.864	0.303	0.362	0.000	0.000	0.131	0.666	0.181	0.333	0.000	0.033*
year	0.691	0.802	0.594	0.396	0.222	0.000	0.157	0.594	0.396	0.222	0.000	0.157
loc	0.686	0.353	0.623	0.294	0.333	1.000	0.000	0.332	1.000	0.000	0.000	1.000
substr	0.622	0.729	0.551	0.542	0.222	0.000	0.294	0.551	0.542	0.222	0.000	0.294
temp	0.577	0.801	0.504	0.328	0.444	0.000	0.108	0.506	0.231	0.889	0.000	0.053°

4 CLIMATIC FACTORS INFLUENCING MOVEMENT ABILITY OF *MANTIS RELIGIOSA* AT TWO GERMAN SITES

4.1 Abstract

Despite its high fidelity, the thermophilic insect species *Mantis religiosa* strongly expanded its range across Germany within the past decades. In this study, we examined the movement ability of *M. religiosa* in terms of movement probability and movement distance, and the relationship between movement ability and climatic and biotic factors. We therefore conducted capture-mark-recapture experiments with adult *M. religiosa* and mapped prevailing microclimatic factors over two vegetation periods at two study sites in Germany. To estimate movement probabilities of adults we used Jolly-Seber models. We initially tested whether movement probability and distances differ between sexes, and whether movement distances correlate with relative wing-length. Contrary to other studies on *M. religiosa*, neither movement probabilities nor movement distances were on average larger in males than in females, and movement distance did not increase with increasing relative wing-length. This suggests that our study underestimates the movement ability of males, presumably because both study areas were too small to detect long-distance movement of males. Applying regression analyses, we tested whether temperature affected movement probability and distances of adults (males and females were pooled). Relative humidity correlated highly with temperature at both areas. Our regression analyses revealed that movement probability increases with increasing temperatures. Movement distances decreased with increasing temperature as the sit-and-wait predator *M. religiosa* moved the shortest distances at temperatures under which prey movement was high. Under more thermally unfavorable conditions leading amongst others to low prey densities in the close vicinity of a *M. religiosa* adult, distances increased again because *M. religiosa* searches for prey or shelter. Our results corroborate that ambient temperature considerably influences movement ability of *M. religiosa*.

4.2 Introduction

Within Europe, climatic warming and landscape changes allow many thermophilic Mediterranean species to expand their range into central and northern Europe (Hickling et al. 2006; Parmesan 2006; Walther et al. 2009). The praying mantis *Mantis religiosa* (LINNAEUS, 1758), a thermophilic insect species that is native to Mediterranean and south eastern European regions, also expands into central Europe (Brechtel 1996; Parmesan & Yohe 2003; Liana 2007; Walther et al. 2009; Robinet & Roques 2010; Berg et al. 2011; Linn & Griebeler 2015). Currently, the northern edge of its distribution range in Europe is in France, Germany and southern Poland. In Germany, records of *M. religiosa* continuously shift northwards (Berg et al. 2011). As *M. religiosa* is a sedentary sit-and-wait predator and thus shows a high fidelity, an active colonisation of new habitats seems unlikely. Therefore, the current range expansion of the species is mainly attributed to passive dispersal of single individuals or egg cases (ootheca), which are transported by man, animals or wind (Niehuis & Schulte 1993; Brechtel et al. 1996; Cannings 2007; Liana 2007). Nevertheless, *M. religiosa* is able to actively colonize new nearby habitats (Stärz et al. 2010).

Range expansion of *M. religiosa* is only observed into thermally favourable areas (Berg et al. 2011, Linn & Griebeler 2015). Ongoing climatic warming might increase the frequency and availability of such warm localities, and thus facilitate the successful establishment of new populations (Parmesan et al. 1999, Walther et al. 2002, Sparks et al. 2007, Robinet & Roques 2010). As dispersal often depends on temperature, climate warming might prolong the time period within the year, in which the threshold temperature for flying and walking of individuals is passed, and especially increases the possibility of migration early in the year (Bale et al. 2002).

Anyhow, dispersal in general, and the impact of environmental factors on its dispersal ability are not completely understood in *M. religiosa*, yet. Information on the movement ability of species is important to predict future range distributions of species. The majority of species distribution models established assumes either a full- or no-dispersal scenario. The first scenario is expected to strongly overestimate the future range of the species and the second scenario to underestimate its range (Buse & Griebeler 2011; Bateman et al. 2013).

Here, we study the active movement ability of adult *M. religiosa*, as adults are most important for colonization of a habitat. We analyse how different microclimatic factors affect their movement probability and their movement distance. First analyses on the movement of *M. religiosa* were conducted by Ehrmann (1985), Hideg (1994), Liana (2007) and Stärz et al. (2010). Liana (2007) generally found that environmental changes caused migration of *M. religiosa*. Stärz et al. (2010) studied the movement of larvae and of adult *M. religiosa*. They found an age-dependent effect on the movement of larvae and adult *M. religiosa* but did not explicitly analyse the influence of the microclimatic factors temperature and relative humidity on the movement.

To assess the influence of climatic factors on movement probability and movement distance of *M. religiosa*, we performed capture-mark-recapture studies for adult *M. religiosa* at two sites during two growing seasons (summer 2011 and summer 2012). Simultaneously, we monitored the environmental parameters temperature and relative humidity with data loggers at each of the sites.

Adult *M. religiosa* show a high fidelity under sufficient food supply and optimal habitat conditions (Ehrmann 1985; Hideg 1994; Liana 2007). As warmer temperatures increase the activity of many of its prey species (Bale et al. 2002), we expected that raising temperature decrease the movement of adult *M. religiosa*. After reaching an optimum temperature higher temperatures will increase movement again, as these are harmful to *M. religiosa* itself. As high relative humidities, such as during precipitation, are suboptimal for the prey species and *M. religiosa* itself, we expected that the movement of adult *M. religiosa* would increase with increasing relative humidities. However, the latter hypothesis implicitly assumes that temperature is not limiting the movement of *M. religiosa*.

4.3 Material and Methods

4.3.1 Study species Mantis religiosa

Mantis religiosa inhabits warm, open, dry and prey-rich habitats in the Afrotropis, and in the southern Palearctis and Orientalis (Stärz et al. 2010; Berg et al. 2011). As sit-and-wait predator *M. religiosa* mostly feeds on arthropods (Reitze & Nentwig 1991; Klass & Ehrmann 2005; Stärz et al. 2010; Berg et al. 2011) and has under sufficient food supply a relatively small home range. *Mantis religiosa* shows aggressive territorial behaviour, sometimes resulting in cannibalism (Hideg 1994). Under insufficient food supply, *M. religiosa* changes sites in order to escape areas of low food availability (personal observations). A similar foraging behaviour is also seen in wolf spiders (Kruse et al. 2008).

4.3.2 Study sites

We studied two *M. religiosa* populations in south western Germany (Weyher, N 49.268 E 8.084 and Pleisweiler, N 49.116 E 8.003; Fig. 4.1) over two summers (2011 and 2012). Both study sites were former vineyards and are now open dry fallow land. On each site, we surveyed a marked-out study area. We divided each study area in grid cells of 2 x 2 m (Fig. 4.1). In Weyher, the marked-out study area measured ca. 144 m^2 whereas in Pleisweiler the study area measured ca. 352 m^2.

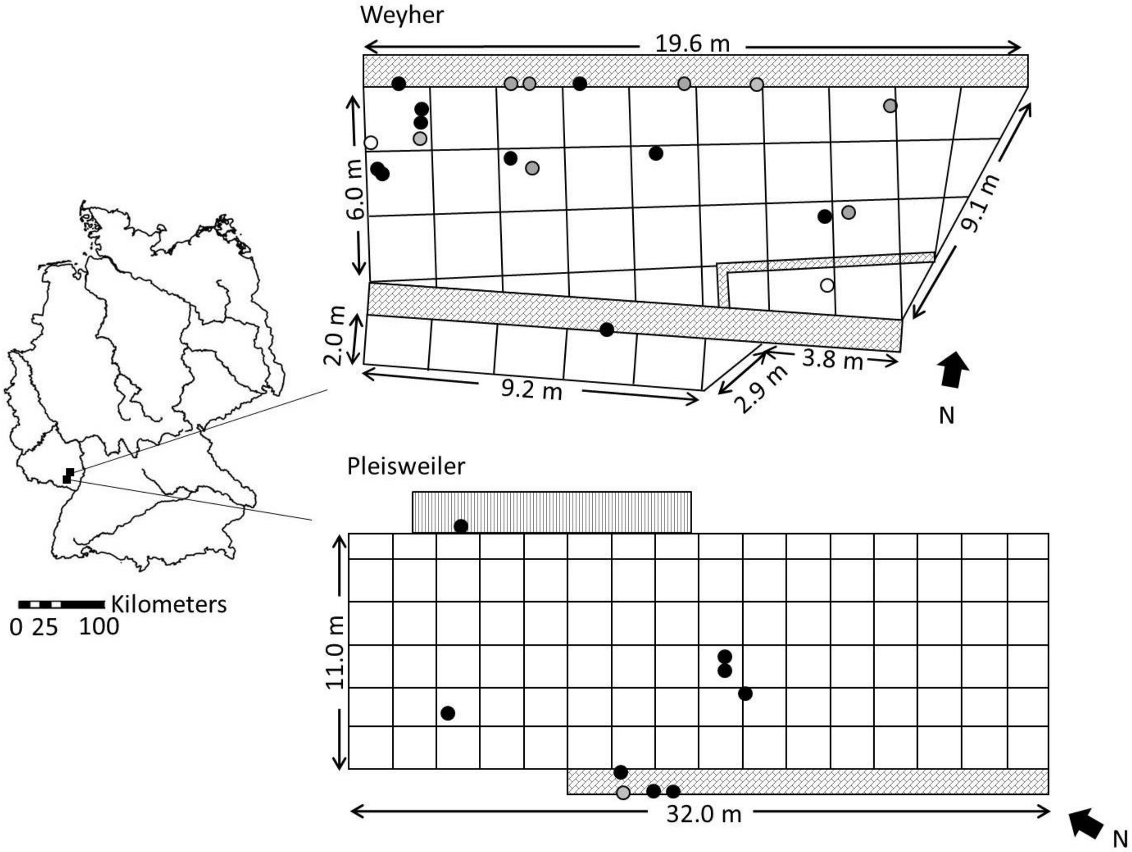


Fig. 4.1. Study sites Weyher and Pleisweiler in western Germany. The marked-out study areas were divided in grid cells of ca. 2 x 2 m. Shown are the grid cells, major environmental structures (lined box: pile of logs, bricked boxes: stone walls) and positions of data loggers (dots). Dot colors represent the time period of measurements: black dots represent recording of temperature and relative humidity during both study periods (2011 and 2012), white dots represent recordings in 2011, and grey dots represent recordings in 2012. During our study we had to replace data loggers due to malfunction or loss of data loggers.

4.3.3 Data collection

4.3.3.1 Environmental factors

To hourly record the temperature (in °C), and relative humidity (in %) in Weyher and Pleisweiler, we installed in total 33 data loggers (TGP-4500 and TGP-4505, Tinytag, Gemini Data Loggers) at different substrates (blank earth without vegetation; hard substrates, e.g. stones, dry stone walls, metal poles; woody plants; herbaceous plants) in the grid cells (Fig. 4.1). For further information on the frequencies of substrates at study sites and differences in their microclimatic conditions, please refer to Linn & Griebeler (in review; Kapitel 3).

4.3.3.2 Capture-mark-recapture experiments

In order to assess the movement of adult *M. religiosa*, we carried out a capture-mark-recapture study with adult *M. religiosa* at both study sites. Therefore, we weekly controlled each grid cell of both marked-out study areas systematically for adult presence in the periods July to October 2011 and July to October 2012 (12 sampling occasions/ days in each study year). All newly found adult *M. religiosa* were marked with a number to identify individuals later. For each captured individual we noted its individual number, the grid cell of the area in which it was found, as well as the day of capture (hereafter sampling occasion, *occ*; Table 4.1), and the study year (*year*). Additionally, we noted the sex (*sex*), body size and wing size of the captured animal in order to assess the potential influence of these characteristics on the movement of individuals. Each individual was released at the same position where it was found.

4.3.4 Statistical analyses

4.3.4.1 Environmental factors

We assessed the influence of microclimatic factors on movement distance and movement probability. We considered microclimatic factors in distinct periods.

For movement distance, we generated for each of the four substrates in each study area and study year a single temperature series and a single humidity series containing hourly values (4 substrates x 2 climatic factors x 2 years = 16 series per area). We chose this approach due to logistical limitations in the number of data loggers. We then calculated the daily mean temperature and humidity of each substrate by averaging the hourly recorded values of all data loggers, which were installed in the same substrate at a site. From these daily mean temperatures we then calculated the average temperature and average humidity for the period between the two captures of an individual ($temp_{capt}$, hum_{capt}; Table 4.1) to assess microclimatic effects on the individual movement distance. As we did not always recapture individuals the next occasion day but up to several weeks later, we considered the microclimatic factors of the substrate and the area at which the individual was recaptured for the period between two consecutive captures.

For movement probability of *M. religiosa*, we considered overall climatic effects of the sites. Therefore, we calculated for each study area a single temperature and single humidity series. In these series, mean daily temperatures and humidities of all substrates were averaged thereby controlling for the frequency of substrates observed at a study site (weighted mean). From these series, we derived the parameters $temp_{occ}$, and hum_{occ} (Table 4.1) reflecting overall temperature and humidity of the period between the sampling occasions. For movement probability we considered the microclimatic factors between the sampling occasions, i.e. the microclimatic factors of the respective previous week to each sampling occasion.
To assess overall limiting microclimatic conditions for movement distance and probability of adult *M. religiosa* we further calculated the arithmetic mean of the daily maximum temperatures and of the daily minimum humidities for the period between two consecutive captures ($temp_{max\_capt}$, hum_{min_capt}) and for the period between the sampling occasions ($temp_{max\_occ}$, hum_{min_occ}; Table 4.1). The main activity period of *M. religiosa* is during daytime (Dohle & Westheide 1996), so that the maximum temperature and minimum relative humidity of a day determine the main activity period of *M. religiosa.* The parameters $temp_{max\_capt}$, $hum_{min\_capt,}$ $temp_{max\_occ}$ and hum_{min_occ} are averages over daily values within the respective periods and were derived from the temperature and humidity values directly recorded by the data loggers during the respective period in the study area. The maximum temperature of a day is the highest temperature measured at this day by any of the data loggers installed at the site. The minimum humidity of a day is the lowest relative humidity measured at a day by any of these data loggers.

To generally explore the interaction in temperature and relative humidity on our study sites, we conducted for each study area Spearman-Rank correlation analyses in the software SPSS Statistics (IBM, version 21). We tested for each study area if the daily weighted mean temperatures and relative humidities correlate over the complete study periods in 2011 and in 2012. We also tested for both periods if daily maximum temperatures and weighted daily mean temperatures correlate and if daily maximum temperatures and minimum relative humidities correlate.

4.3.4.2 Movement analysis

Body length and wing length. All individuals did slightly differ in their body length and wing length. Hence, we calculated for each individual its relative wing length (WL_{rel}) as the quotient of its wing length and body length. We used the paired Wilcoxon test (SPSS Statistics) to explore differences in wing length, body length, and relative wing length between males and females.

Travelled distance. We determined the simple travelled distance (in meter) of each recaptured *M. religiosa* individual between two consecutive captures in ArcMap (ArcGIS version 10.2.0.3348). If more than one week was between the two captures, we standardised the movement distance of an individual to a weekly distance.

We examined possible differences in the travelled distance of males and females in Kruskal-Wallis tests (SPSS Statistics). As relative wing length is known to affect the migration ability of insects (Kingslover & Koehl 1985) and females and males differed in relative wing lengths (see Results), we conducted a Spearman-Rank correlation between relative wing length and mean travelled distance for males and females, separately (SPSS Statistics).

To roughly estimate the movement of *M. religiosa* during its adult phase, we exemplary estimated the home range from minimum convex polygons (MCP) for four female *M. religiosa* that were at least five times captured (statistical minimum). We captured all other imagines less frequently. We calculated the MCPs in R (version 2.14.2, R Core Team 2012) from the capture positions of animals, using the package ‘adehabitatHR’ (version 0.4.11) and ‘sp’ (version 1.0-14). All MCPs were calculated after the removal of 5% of extreme points or at least of one point.

4.3.4.3 Population size and probability of entrance

Based on the encounter histories of each individual, we estimated the population sizes for the two study areas using the program MARK, version 7.1 (Lebreton et al. 1992; White et al. 2001). Here, we used the sub-module POPAN (Schwarz & Arnason 1996), which calculates Jolly-Seber models and is suitable for open populations. POPAN estimates the survival probability between captures (Φ) for individuals of a studied population, and estimates the recapture probability (p) for individuals at each sampling occasion. Furthermore, POPAN estimates the probability of entrance (b) of individuals from a super population (i.e. all animals that would ever enter the population or would be born; Schwarz & Arnason 1996) into the studied population between two sampling occasions. From these estimates, the total population size (N) and the gross weekly entrants (*B*-hat*) of *M. religiosa* are derived by MARK for the studied population. We established a separate model for each study area and each study period as both areas considerably differed in size. As *M. religiosa* is univoltine, and we only observed a few imaginal moultings at both study areas (between the first and the fifth sampling occasion), we assumed that the entrance of individuals in both populations was mostly due to immigration and not birth. Hence, we used the estimated weekly entrants (“gross birth and immigration estimates”, *B*-hat*) as a measure of movement probability of individuals within a week.

We started modelling in MARK with the most parameterized model. We used a model with full time ($_t$) and sex ($_g$) dependence of survival, recapture and entrance probabilities ($\Phi_{(t*g)}p_{(t*g)}b_{(t*g)}$). From this, we developed more general candidate models by reducing the number of model parameters. We tested the interaction between time and sex ($_{t*g}$), and further tested time ($_t$) and sex ($_g$) independently. We also tested each possible combination of model parameters (Online Resource 4.1). Unfortunately, our data set on encounter histories was too small (n = 32 up to n = 91) to calculate the effect of microclimatic predictor variables (Table 4.1) on the weekly entrances (*B*-hat*) in MARK. For Pleisweiler, in 2012 the data set on encounter histories was even too small to run models testing an intersexual difference on the survival, recapture and entrance probabilities.

We used the Akaike Information Criterion (adjusted for small sample size, AIC_C; Akaike 1979) to find the best fitting model derived from MARK. The lowest AIC_C revealed the best model (Burnham & Anderson 2004).

To evaluate the goodness-of-fit (GOF) of the most parameterized model we used the program RELEASE (Version 3.0, Burnham et al. 1987). RELEASE tests the assumption that all marked individuals of a study area and study period have the same survival and recapture probabilities.

4.3.4.4 Predictor variables effecting movement

In order to find an effect of environmental parameters (i.e. time, location, microclimate) and biotic parameters (i.e. sex, size) on the movement of *M. religiosa* we carried out regression analyses in R (version 2.14.2, R Core Team 2012). With these analyses we assessed movement of *M. religiosa* individuals in terms of both the movement probability (derived from *B*-hat*, the gross weekly entrants into the population), and the individual movement distance, i.e. the weekly travelled distance of individuals. We tested the significance of predictor variables listed in Table 4.1 on the movement probability and movement distance in univariate and multivariate models. However, as no model was significantly multivariate, we only consider univariate models from hereon.

Table 4.2. Predictor variables used for modelling movement probability (▲) and movement distance (♦) of *M. religiosa*. Listed are variables recorded in field, the predictor variables derived from these and used for modelling, the abbreviations of predictor variables, and the description of variables.

Variables	**Predictor variables**	**Abbreviations**	**Further descriptions**
sex	male = 1, female = 2	$sex^{\blacklozenge}$	sex of captured *M. religiosa* individual
size	relative wing length	$WL_{rel}^{\blacklozenge}$	ratio of wing length to body length of individual
temperature	mean temperature between sampling occasions	$temp_{occ}^{\blacktriangle}$	weighted mean temperature between sampling occasions at the study site (°C)
	mean temperature between captures	$temp_{capt}^{\blacklozenge}$	mean temperature between two captures, of substrate where individual was recaptured (°C)
	maximum temperature between sampling occasions	$temp_{max\_occ}^{\blacktriangle}$	mean of daily maximum temperatures of study site between sampling occasions (°C)
	maximum temperature between captures	$temp_{max\_capt}^{\blacklozenge}$	mean of daily maximum temperatures between two captures at the study site (°C)
relative humidity	mean relative humidity between sampling occasions	$hum_{occ}^{\blacktriangle}$	weighted mean relative humidity between sampling occasions at the study site (%)
	mean relative humidity between captures	$hum_{capt}^{\blacklozenge}$	mean relative humidity between two captures, of substrate where individual was recaptured (%)
	minimum relative humidity between sampling occasions	$hum_{min\_occ}^{\blacktriangle}$	mean of daily minimum relative humidities of study site between sampling occasions (%)
	minimum relative humidity between captures	$hum_{min\_capt}^{\blacklozenge}$	mean of daily minimum relative humidities between two captures at the study site (%)
sampling occasion	day 1 to 12 of encounter history	$occ^{\blacktriangle\blacklozenge}$	day of capture-mark-recapture experiment
study period	2011, 2012	$year^{\blacklozenge}$	year in which capture-mark-recapture experiment was conducted
study site	Pleisweiler = 1, Weyher = 2	$loc^{\blacklozenge}$	location of capture-mark-recapture experiment

4.3.4.5 Movement probability

In order to identify the environmental variables affecting the movement probability of *M. religiosa*, we carried out logistic regression analysis assuming binomial distributed errors for both study areas. As an estimate of movement, we used the “gross birth and immigration estimates” (*B*-hat*) for each sampling occasion derived from the best-supported model of each study area and study period. These estimates are found in the MARK output and assess the number entrants into the studied population. To transform these real numbers to a binary information which is required for logistic regression analysis, we set all “gross birth and immigration estimates” > 0.5 to 1 (movement present) and all < 0.5 to 0 (movement absent).

As during the first sampling occasion, besides immigration, imaginal moulting might have caused an entrance of individuals into the populations, we excluded in these logistic regression analyses the days at which we observed imaginal moulting (Pleisweiler 2011: sampling occasions 1 through 5; 2012: sampling occasions 1 and 2; Weyher 2011: sampling occasions 1 through 4; 2012: sampling occasions 1 and 2).

In our logistic regression analyses we considered the predictor variables $temp_{occ}$, $temp_{max\_occ}$, hum_{occ}, hum_{min_occ}, and *occ* (Table 4.1), in order to find an effect of previous week weather on the movement probability of *M. religiosa*.

4.3.4.6 Movement distance

In order to detect environmental factors affecting the movement distance of *M. religiosa,* we carried out regression analysis with $\log_{10}$-transformed travelled distances and the predictor variables *sex*, WL_{rel}, $temp_{capt}$, $temp_{max\_capt}$, hum_{capt}, hum_{min_capt}, *occ, year* and *loc* (Table 4.1). We log-transformed our dataset to comply the conditions for regression analyses with normally distributed residuals. The dataset on movement distance consisted of distances that animals travelled at both study areas and during both study periods. As we could not determine all substrates, which a *M. religiosa* individual used between captures in our study areas, the variables $temp_{capt}$, $temp_{max\_capt}$, hum_{capt}, hum_{min_capt} were derived from the temperature and humidity series of the substrate and the area at which the individual was recaptured.

4.3.4.7 Preparation and evaluation of regression analyses on movement

We selected candidate regression models for movement based on their significant deviation from the null model and only for logistic regression models whether they were not affected by over or under dispersion (phi between 0.8 and 1.2). To test whether regression models differ from the null model we conducted likelihood ratio tests. We chose the final best model according to its AIC value (Akaike Information Criterion, Akaike 1979; lowest AIC value, Burnham & Anderson 2004). The goodness-of-fit of a model was identified from Nagelkerke's R^2 (R^2_N; package 'fmsb', version 0.3.8, R).

We carried out all regression analyses, tests for over or under dispersion and likelihood ratio tests in the software R (version 2.14.2, R Core Team 2012). For all regression analyses, we used the standard settings for general linear models (glm, package 'stats' version 2.14.2).

4.4 Results

4.4.1 *Field work*

4.4.1.1 Temperature and relative humidity

We found no difference in the weighted mean summer temperature (study period July 15th to October 11th 2011 and July 30th to October 15th 2012) within each study area between both study periods. Contrary, relative humidity significantly differed between both periods (Table 4.2). In both periods, the marked-out study area in Weyher was warmer and dryer than in Pleisweiler (Table 4.2).

We measured maximum temperatures up to 60°C at both study areas, as close to the ground the sun heat accumulated. *Mantis religiosa* individuals, however, most probably were not exposed to such high temperatures.

Table 4.2. Mean temperatures and relative humidities for both study areas during both study periods (July 15th - October 11th 2011, July 30th - October 15th 2012). (a) Weighted mean temperature ± standard deviation (SD) and weighted mean relative humidity ± SD; (b) Results from paired Student t-tests and Wilcoxon-tests, respectively. For each study area differences between years are tested and finally sites are compared for each year; shown are t_{test}-values (t_{test}), U-values▲ (U), degrees of freedom (df) and P-values with significance levels. Significant tests are highlighted ° P ≤ 0.1; *** P ≤ 0.001.

(a) Rawdata	**Temperature (°C) ± SD**	**Relative humidity (%) ± SD**
Pleisweiler 2011	18.07 ± 3.46	86.38 ± 7.35
Pleisweiler 2012	18.16 ± 5.01	76.62 ± 8.11
Weyher 2011	19.11 ± 4.28	79.24 ± 12.82
Weyher 2012	18.92 ± 5.28	77.33 ± 11.33

(b) Statistical analyses	**t_{test}**	**df**	**P**	**t_{test} or U**	**df**	**P**
Pleisweiler: 2011 vs. 2012	0.638	77	0.526	-5.491▲	78	< 0.001***
Weyher: 2011 vs. 2012	-1.348	77	0.181	1.969	77	0.053°
2011: Pleisweiler vs. Weyher	-9.929	88	< 0.001***	-7.583▲	89	< 0.001***
2012: Pleisweiler vs. Weyher	-5.722	77	< 0.001***	-0.789▲	78	0.430

The weighted daily mean temperature and weighted daily mean relative humidity correlated at each study area in both study periods (Table 4.3). In addition, the daily weighted mean temperature and the daily maximum temperature as well as the daily maximum temperature and daily minimum relative humidity correlated at each study area during both study periods (Table 4.3).

Table 4.3. Spearman-Rank correlation of temperature and relative humidity for the study areas Weyher and Pleisweiler in both study periods 2011 and 2012. Shown are the Spearman Rank correlation coefficient (r_S), number of variables (n) and significance level (P). Significances are highlighted *** P ≤ 0.001.

	Mean temperature vs. mean relative humidity			**Mean temperature vs. maximum temperature**			**Maximum temperature vs. minimum relative humidity**		
	r_s	**n**	**P**	**r_s**	**n**	**P**	**r_s**	**n**	**P**
Pleisweiler 2011	-0.377	89	< 0.001***	0.603	89	< 0.001***	-0.823	89	< 0.001***
Pleisweiler 2012	-0.674	78	< 0.001***	0.843	78	< 0.001***	-0.728	78	< 0.001***
Weyher 2011	-0.580	89	< 0.001***	0.825	89	< 0.001***	-0.747	89	< 0.001***
Weyher 2012	-0.854	78	< 0.001***	0.904	78	< 0.001***	-0.549	78	< 0.001***

4.4.1.2 Mantis religiosa

Populations. In Weyher, we captured in total 132 times *M. religiosa* individuals. In Pleisweiler, we captured in total 183 times *M. religiosa*. In both study periods the recapture rate was higher in Weyher than in Pleisweiler. Females were more often recaptured than males (Table 4.4).

In total, we recorded in both study areas during both years 113 movements of 203 *M. religiosa* imagines. This yielded encounter histories on 12 sampling occasions in both years.

The best-supported model in MARK estimated for Weyher a super population size of 53.408 ± 7.619 SE (standard error) in 2011 and of 82.229 ± 10.935 SE in 2012. In Pleisweiler, the estimated size of the super population was 175.913 ± 19.021 SE in 2011 and of 48.823 ± 6.400 SE in 2012. Hence, in Weyher we marked in 2011 60%, and in 2012 58% of the population. In Pleisweiler, we marked in 2011 52% and in 2012 66% of the population (Table 4.4).

Body length and wing length. Mean body length and wing length of females was significantly larger than of males. Although the relative wing length (WL_{rel}) of males was significantly larger than of females (Table 4.4 and 4.5), it did not correlate with the mean travelled distance of individuals (Spearman-Rank correlation: males: r_s = -0.036; n = 30; P = 0.850; females: r_s = -0.220; n = 47; P = 0.137).

Table 4.4. Number of captures, movement and size of *M. religiosa* males and females for the study areas Pleisweiler and Weyher in both study years. Shown are the number of newly found *M. religiosa* imagines, number of recaptures and recapture rates. Further shown is the mean distance between captures, calculated as mean weekly movement of *M. religiosa* (in meter, m) with standard deviation (SD), the mean body length (in millimeter, mm), mean wing length (in mm), and mean relative wing length with SD for males and females.

	Pleisweiler				**Weyher**			
	2011		**2012**		**2011**		**2012**	
	♂	♀	♂	♀	♂	♀	♂	♀
No. of first captures	43	48	15	17	19	13	22	26
No. of recaptures	15	33	3	10	6	14	10	22
Recapture rates	0.349	0.688	0.200	0.588	0.316	1.077	0.455	0.846
Mean weekly movement (in m)	4.007 ± 3.399 SD	5.332 ± 3.593 SD	5.947 ± 7.677 SD	3.153 ± 2.866 SD	3.614 ± 4.389 SD	3.423 ± 3.325 SD	5.666 ± 6.400 SD	4.877 ± 3.855 SD
Mean body length (in mm)	47.330 ± 2.851 SD	55.287 ± 3.373 SD	45.767 ± 3.812 SD	54.735 ± 2.444 SD	46.389 ± 3.116 SD	57.192 ± 3.935 SD	47.386 ± 2.493 SD	56.038 ± 3.292 SD
Mean wing length (in mm)	35.772 ± 2.521 SD	38.675 ± 2.876 SD	33.167 ± 2.876 SD	38.118 ± 2.081 SD	34.521 ± 2.006 SD	39.385 ± 1.938 SD	34.459 ± 2.095 SD	39.269 ± 2.367 SD
Mean relative wing length	0.756 ± 0.041 SD	0.700 ± 0.039 SD	0.726 ± 0.045 SD	0.696 ± 0.024 SD	0.746 ± 0.048 SD	0.691 ± 0.048 SD	0.727 ± 0.029 SD	0.702 ± 0.037 SD

Table 4.5. Results of the Wilcoxon tests on differences in body length, wing length and relative wing length between males and females on both study areas and study periods. Shown are U-values (U), degrees of freedom (df) and P-values with significance levels. Significant tests are highlighted * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

	Pleisweiler						**Weyher**					
	2011			**2012**			**2011**			**2012**		
	U	**df**	**P**	**U**	**df**	**P**	**U**	**df**	**P**	**U**	**df**	**P**
Body length	-5.450	41	< 0.001***	-3.357	13	0.001***	-3.183	11	0.001***	-4.046	20	< 0.001***
Wing length	-3.547	41	< 0.001***	-3.205	13	0.001***	-3.063	11	0.002**	-4.017	20	< 0.001***
Relative wing length	-4.878	41	< 0.001***	-1.988	13	0.047*	-2.760	11	0.006**	-2.159	20	0.031*

4.4.2 Movement

4.4.2.1 Travelled distances

The distribution of weekly travelled distances of male and female *M. religiosa* followed a leptokurtic curve (Fig. 4.2). Adult *M. religiosa* moved on average within one week between 3.153 m ± 2.866 SD and 5.947 m ± 7.677 SD (Table 4.4). The mean weekly travelled distance did not differ between male and female *M. religiosa* (Kruskal-Wallis test: χ^2 = 2.736; df = 1;

P = 0.098) nor between study areas or study periods (Kruskal-Wallis test: study areas: χ^2 = 0.829; df = 1; P = 0.363; study periods: χ^2 = 0.082; df = 1; P = 0.775).

The longest measured travelled distance between two captures was observed for a male in Weyher in 2012 and was 22.59 m within the week. The shortest travelled distance between two captures was also observed for a male in Weyher in 2012, and was 0.47 m within the week.

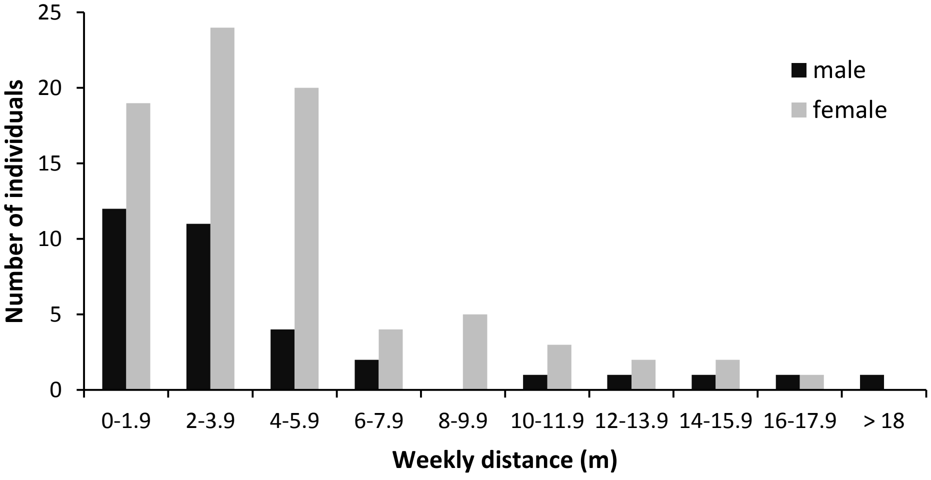


Fig. 4.2. Weekly travelled distances of male (black bars) and female (grey bars) *M. religiosa* pooled from both study areas Pleisweiler and Weyher and both years 2011 and 2012.

The mean home range of the four exemplary evaluated *M. religiosa* females (three females in Pleisweiler, one female in Weyher) was 5.375 m^2 ± 1.843 SD (Table 4.6).

Table 4.6. Home range of four individuals (females) from the study areas Pleisweiler and Weyher. Shown is the origin of the individuals (study area), the period in which the individual was captured several times, number of weeks covered by this period, the number of captures of the animal during this period, and the home range size of the individual derived from the minimum convex polygon (MCP) of its roosting sites.

Study area	Capture period	No. weeks	No. captures	Home range
Pleisweiler	Aug 8th, 2011 – Sept 27th, 2011	7	5	5.5 m^2
Pleisweiler	Aug 1st, 2011 – Aug 29th, 2011	4	5	5.5 m^2
Pleisweiler	Aug 7th, 2012 – Sept 11th, 2012	5	5	3 m^2
Weyher	Aug 6th, 2012 – Oct 15th, 2012	10	5	7.5 m^2

4.4.2.2 Population size, probability of survival, probability of recapture and of entrance

In terms of AIC_C (Akaike 1979; Table 4.7), the model $\Phi(.)p(.)b_{(t)}$ described best the encounter histories of *M. religiosa* individuals for both study areas and study periods. This model assumes a constant survival $\Phi(.)$ and recapture probability $p(.)$, and a time dependent probability of entrance $b_{(t)}$. Models, which consider an intersexual difference in Φ, p, and b, were less supported in terms of AIC_C (Online Resource 4.1).

The assumption that each marked individual has the same recapture and survival probability could not be tested with the GOF test due to insufficient large sample size at both study areas in both study periods. Hence, all results based on MARK models should be considered with caution. Nevertheless, the identical model repeatedly described best the encounter history of all studied populations, which confirms the reliability of our data (Table 4.7).

Table 4.7. Statistics of models created to assess the effect of time ($_t$) and sex ($_g$) on the survival probability (Φ), recapture probability (p) and the entrance probability (b) for *M. religiosa* individuals for each study area and each study period. Shown are the three best models, chosen and ranked according to their AIC_c (Akaike's information criterion corrected for small samples, Akaike 1979; Burnham & Anderson 2004). The three best models did not show any intersexual difference in Φ, p, and b. Further shown are the number of model parameters (K) and the deviance of the models. The index ($_.$) represents time independence. Due to an insufficient sample size, we could not conduct a goodness-of-fit (GOF) test to test for an equal recapture and survival probability among individuals.

Model	AIC_C	K	Deviance
Pleisweiler 2011			
$\Phi_{(.)}p_{(.)}b_{(t)}$	322.859	13	293.947
$\Phi_{(t)}p_{(.)}b_{(t)}$	333.938	23	278.338
$\Phi_{(t)}p_{(.)}b_{(.)}$	365.761	23	310.161
Pleisweiler 2012			
$\Phi_{(.)}p_{(.)}b_{(t)}$	120.477	13	0.000
$\Phi_{(.)}p_{(.)}b_{(.)}$	141.108	13	0.000
$\Phi_{(t)}p_{(.)}b_{(t)}$	175.740	23	0.000
Weyher 2011			
$\Phi_{(.)}p_{(.)}b_{(t)}$	161.694	13	126.361
$\Phi_{(.)}p_{(.)}b_{(.)}$	185.326	13	149.993
$\Phi_{(t)}p_{(.)}b_{(t)}$	191.451	23	107.383
Weyher 2012			
$\Phi_{(.)}p_{(.)}b_{(t)}$	236.698	13	205.183
$\Phi_{(t)}p_{(.)}b_{(t)}$	256.553	23	190.839
$\Phi_{(.)}p_{(.)}b_{(.)}$	261.308	13	229.793

4.4.3 Predictor variables effecting movement

For the regression analysis on movement probability and distance, we combined the data from both study periods and both study areas to increase the sample size.

4.4.3.1 Movement probability

The movement probability of *M. religiosa* was best described by the univariate logistic regression models *occ* (AIC = 34.093, R^2_N = 0.446) and $temp_{occ}$ (AIC = 34.277, R^2_N = 0.441; Table 4.8). The movement probability decreased with proceeding time (*occ*) and increased with increasing temperature ($temp_{occ}$). At $temp_{occ}$ of 27°C, the movement probability almost equals 1. The univariate models with variables $temp_{max\_occ}$ (AIC = 40.096, R^2_N = 0.256) and hum_{occ} (AIC = 41.352, R^2_N = 0.211; Table 4.8) were less supported in terms of AIC and R^2_N.

4.4.3.2 Movement distance

The regression analyses revealed that temperature between the captures mostly affected the travelled distance of *M. religiosa*. The best models tested for movement distance were $temp_{max\_capt} + temp_{max\_capt}^2$ (AIC = 81.838, R^2_N = 0.103) and $temp_{\_capt} + temp_{\_capt}^2$ (AIC = 82.742, R^2_N = 0.096, Table 4.8). *Mantis religiosa* moved least at a $temp_{max\_capt}$ of ca. 45°C and at $temp_{capt}$ of ca. 20°C. Below and above these temperatures movement increased. The model *occ* (AIC = 87.827, R^2_N = 0.034) was less supported in terms of AIC and Nagelkerke's R^2_N. All models had a very low variance explained. All other predictor variables (Table 4.1) had no effect on the movement distance of *M. religiosa*.

Table 4.8. Logistic regression models for movement probability and regression models for movement distance of *M. religiosa*. Field data on *M. religiosa* movement were pooled from both study areas and both study periods to establish models. Data of movement distance were $\log_{10}$-transformed. All models significantly deviating from the null model are shown. Selection of models was based on AIC (Akaike information criterion; ΔAIC approach, Burnham & Anderson 2004) and Nagelkerke's R^2 (R^2_N) values. Logistic regression models of movement probability were neither subject to model over nor under dispersion. Shown are AIC values with degrees of freedom (df_{AIC}), R^2_N with degrees of freedom ($df_{R^2_N}$), values of estimated regression coefficients (β values) with standard errors (SE), and the intercept with SE. Significant predictor variables are highlighted ° P < 0.1; * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

Models	**AIC**	**df_{AIC}**	**R^2_N**	**$df_{R^2_N}$**	**β1 ± SE**	**β2 ± SE**	**Intercept ± SE**
Movement probability							
β1 occ	34.093	29	0.446	31	-0.691 ± 0.247**		5.543 ± 2.009**
β1 $temp_{occ}$	34.277	29	0.441	31	0.456 ± 0.169**		-8.388 ± 3.187**
β1 $temp_{max\_occ}$	40.096	29	0.256	31	0.132 ± 0.059*		-5.241 ± 2.456*
β1 hum_{occ}	41.352	29	0.211	31	-0.131 ± 0.062*		10.407 ± 4.921*
Movement distance							
β1 $temp_{max\_capt}$ + *β2* $temp_{max\_capt}^2$	81.838	111	0.103	114	-0.162 ± 0.047***	0.002 ± 0.001***	4.011 ± 1.003***
β1 $temp_{capt}$ + *β2* $temp_{capt}^2$	82.742	111	0.096	114	-0.317 ± 0.095**	0.008 ± 0.002**	3.622 ± 0.939***
β1 occ	87.827	112	0.034	114	0.024 ± 0.012°		0.406 ± 0.073***

4.5 Discussion

We marked approximately between 52% and 66% of the studied populations. These high recapture rates support the hypothesis that the sit-and-wait predator *M. religiosa* is very sedentary (Ehrmann 1985; Hideg 1994; Liana 2007) but also indicate a high quality of the two habitats.

The main factors influencing movement of *M. religiosa* were temperature and time. An influence of climatic factors on movement is common among insect species (Cammell & Knight 1992; Bale et al. 2002). Temperature and relative humidity correlated at our study sites, and reflect the overall weather conditions. Hence, an effect of humidity on movement is also possible, although it was less supported in the models.

We developed our regression models for adult movement based on the environmental conditions recorded in our marked-out study areas. As these conditions only comprise a small subset of possible temperatures and relative humidity for *M. religiosa* habitats, the application of our models to other geographic regions is limited due to the risk of model extrapolation.

4.5.1 Movement

4.5.1.1 Movement probability

The best models derived in MARK describing the encounter histories of *M. religiosa* individuals revealed a time dependence of the entrance probability of individuals into the populations. The logistic regression analyses also suggested a temporal effect on the movement probability of *M. religiosa*. The movement probability decreased with proceeding sampling occasions. This could reflect an individual age effect. Hideg (1991) observed in captivity, under optimal conditions a maximum life span of 257 days for female and 189 days for male *M. religiosa* (average life span of females: 210 days; of males: 175 days). However, as in our studied populations (first larvae observed in mid-May and last imago observed in mid-October, Linn & Griebeler, in review; Kapitel 3) such maximum life spans were not reached, we assume that the time dependence of movement most likely results from decreasing temperatures later during the course of the year. Our interpretation is supported by the observation that logistic regression models also revealed an effect of temperature on the movement probability of *M. religiosa*, as well as by field observations on *M. religiosa* (Liana 2007) and other insects (Heinrich 1974; Kemp 1986; Cammell & Knight 1992; Bale et al. 2002). Increasing temperatures increase the activity of insects and thus individuals show a greater tendency to move (Walters et al. 2006).

Likewise, the frequency of site-changes of other sit-and-wait predators increases with temperature (Ford 1978; Bailey 1989; Kruse et al. 2008).

Contrary to our expectations, we did not find any intersexual effect on the probability of entrance in MARK and hence on the movement probability of adult *M. religiosa.* We expected that male *M. religiosa* would show a higher movement probability while searching for a mate (Hideg 1994; Gemeno et al. 2005) than females, which are more sedentary due to increasing body weight for egg production (Detzel & Ehrmann 1998). Furthermore, males have a higher startle response and escape more quickly (personal observation) than the territorial aggressive female *M. religiosa* (Hideg 1994). Obviously, our marked-out study areas were too small to sufficiently recapture the broader travelling males (Detzel & Ehrmann 1998; Liana 2007), what might have caused an underestimation of movement probability for males.

4.5.1.2 Movement distance and home ranges

We checked the study areas only weekly and estimated the travelled distance of individuals from the straight distance between two capture positions. This presumably underestimates the movements distances of individuals and their home ranges, as movement between captures is completely neglected, e.g. due to a switching of the hunting and roosting sites.

The weekly travelled distances of male and female *M. religiosa* followed a leptokurtic distribution (Fig. 4.2). The tail thickness of a leptokurtic dispersal curve is used as a measure of the probability of long-distance movements (Walters et al. 2006). The tail of both dispersal curves are rather thin, which is consistent with the hypothesis that this species shows a low dispersal probability (Ehrmann 1985; Hideg 1994; Liana 2007). Overall, for males and females the mean weekly travelled distances were low (between 3.153 m ± 2.866 and 5.947 m ± 7.677).

In comparison to that, smaller orthoptera species have even a wider movement range: Male Roesel's bush-cricket *Metrioptera roeseli* moved within approximately 91 hours between 6.75 and 10.90 m (Berggren 2005), extrapolated to 12.6 to 20.4 m per week. For the flightless rainbow grasshopper *Dactylotum variegatum*, which was recorded in 2 to 3 days intervals, Joern (1983) calculated an average distance per day of 5.3 m, which extrapolates to 37.1 m per week.

Contrary to our expectation, males did not cover larger distances than females, although males had a significantly larger relative wing size than females. Intersexual differences in wing size and movement distances seem to be a general pattern in insects (den Boer 1970; Harrison 1980; Bartley 1982; McLachlan 1985; Malmqvist 2000; Thomas et al. 2001), and in particular in grasshoppers (Kingslover & Koehl 1985; Maes et al. 2006; Walters et al. 2006). Our unexpected result is an artifact of the small size of our marked-out study areas compared to the movement distances seen in *M. religiosa*. Male *M. religiosa* are more slender and can fly larger distances (Hideg 1994; Detzel & Ehrmann 1998; Liana 2007) than the bigger, ponderous females, which mostly move along by walking and climbing (Detzel & Ehrmann 1998). Hence, males could have more easily left the marked-out study areas than female *M. religiosa*. Our interpretation is supported by the lower recapture rates of males than of females, and by our observations during a monthly screening of the periphery (up to 25 m distance to closest grid cells). In this screening we mostly observed an exchange of female *M. religiosa* between the study areas and their periphery. In Pleisweiler, we found in 2011 two marked adults (one male, one female) outside our study area, whereas in 2012, we were unable to document any exchange of individuals between the study area and the periphery. In Weyher, we found in 2011 one marked female in the periphery, and in 2012 we observed three marked females that emigrated from the periphery into our study area. These additional observations suggest that in our study the movement distances of males were stronger underestimated than those of females. Authors who found an intersexual difference in movement distances carried out their capture-recapture studies in larger than our study areas (Hideg 1994; Detzel & Ehrmann 1998; Liana 2007). For males, these studies revealed a mean travelled distance of 150 m (Hideg 1994; Detzel & Ehrmann 1998; Liana 2007). For females, Hideg (1994) and Stärz et al. (2010) observed a considerable smaller distance of less than 30 m during the complete adult phase (August to October), which is more consistent with sizes of our areas and our results.

We were only able to roughly assess the home range of four females. The area narrowed down by the MCPs varied between 3 and 7.5 m^2 covered within an observation period of 4 to 10 weeks. As the size of a home range is habitat dependent (Burt 1943), these small sizes suggest (at least for females) a high quality of the studied habitats, and support that the species shows a high fidelity under suitable habitat conditions. These results further show that the studied habitats offered fine conditions for egg deposition (August to October; Linn & Griebeler, in review; Kapitel 3), as female *M. religiosa* otherwise travel longer distances (up to 30 m in three months) while searching for suitable habitats for egg deposition (Hideg 1994; Berg et al. 2011).

Our regression analyses revealed that the distance travelled between two captures by *M. religiosa* depends on temperature. Also in grasshopper species, which are an important food source of *M. religiosa* (Reitze & Nentwig 1991; Berg et al. 2011) increasing daily maximum temperature and mean ambient temperature promote movement (Arroyo et al. 1985; Walters et al. 2006). For *M. religiosa*, we found a quadratic dependence of movement distance between two captures on daily mean temperatures and daily maximum temperatures. Both temperature series correlated, so that below and above the optimal temperatures movement distances of *M. religiosa* increased (lowest movement distance of 2.9 m per week at daily mean temperature of 20°C and at daily maximum temperature of 45°C). Climatic conditions at our study sites did not reach the threshold when *M. religiosa* becomes inactive, as summarized by Hideg (1991) for some mantid species.

Many sit-and-wait predators including *M. religiosa* (Reitze & Nentwig 1991) reduce their energy consumption by being less active and capturing prey by ambush-hunting. Lower temperatures, e.g. during periods with colder weather, reduce prey movement (Heinrich 1974; Kemp 1986; Bale et al. 2002). Thus under such thermal conditions, *M. religiosa* has often to switch hunting sites in order to find new prey, which increases the distance travelled between two captures (Liana 2007). Contrary, in periods with higher temperatures, prey movement increases (Cammell & Knight 1992; Bale et al. 2002), which may increase the prey's exposure to predation by a waiting *M. religiosa* and thus, makes movement of *M. religiosa* individual more unlikely (compare Olive 1982). High daily mean temperatures with high maximum temperatures reduce prey activity (Williams 1940; Taylor 1963; Heinrich 1974; Kemp 1986), and thus increase again the movement probability of *M. religiosa* in order to find prey. *Mantis religiosa* also avoids very high ambient temperatures, and seeks shade to prevent overheating (Hideg 1991). This thermoregulation behaviour (May 1979) could have added to the increase in the distances travelled under higher temperatures.

4.5.2 Mantis religiosa and climatic warming in Germany

Our study corroborated that the distances actively moved by *M. religiosa* are small and that females show considerably smaller distances than males. Thus, for a successful colonization of new habitats the movement distance of females seem to be more limiting than that of males. Nevertheless, a single female *M. religiosa* can establish a new population by reproducing under facultative parthenogenesis (Hideg 1996). Furthermore, it is known that passive movement, e.g. the drift of flying individuals and the displacement of egg cases and animals covers much larger distances, which considerably adds to the range expansion of *M. religiosa* (Brechtel et al. 1996; Liana 2007; Cungs et al. 2013). However, how important these processes are for range expansion of *M. religiosa* has not been quantified, yet. Further aspects, which are important for a successful colonisation of new habitats by *M. religiosa* and not sufficiently studied, yet, are the influence of the population density on the individual movement (Hideg 1994) and the quality of the habitat (Linn & Griebeler, in review; Kapitel 3). Both aspects are linked again to the survival rates of individuals. Good weather periods during spring, as usually expected under climatic warming, increase the survival rate of *M. religiosa* larvae (Ehrmann 2003; Stärz et al. 2010), and result in high population densities. In order to avoid cannibalisms under high densities (Hideg 1994), not only adults but also nymphs migrate and rapidly colonize adjacent areas (Dingle 1972; Hurd & Eisenberg 1984; Stärz et al. 2010). Our results suggest that increasing average and maximum temperatures will increase the movement probabilities and distances of *M. religiosa*. As under climatic warming an increase in the frequency of suitable habitats for *M. religiosa* is expected in Germany, this will add to the establishment of more populations at the species' northern distribution range margin. Already in the year 2003, in which an extreme summer prevailed all over Europe (Luterbacher et al. 2004), a range expansion of *M. religiosa* was observed (Ehrmann 2003; Liana 2007; Berg et al. 2011).

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4.7 Supplementary material

Online Resource 4.1. Models established to assess the effect of time ($_t$) and sex ($_g$) on the survival probability (Φ), recapture probability (p) and the entrance probability (b) for *M. religiosa* of each study area and each study period. Shown are all tested models, ranked according to their AIC_C (Akaike's information criterion corrected for small samples; Akaike 1979; Burnham & Anderson 2004). For Pleisweiler 2012, the effect of sex was not tested, as the data set on encounter histories was too small. Further shown are the number of model parameters (K) and the deviance of the models. The index ($_.$) represents time independence. Due to an insufficient sample size we could not conduct a goodness-of-fit (GOF) test.

Model	**AIC_C**	**K**	**Deviance**
Pleisweiler 2011			
$\Phi_{(.)}p_{(.)}b_{(t)}$	322.859	13	293.947
$\Phi_{(t)}p_{(.)}b_{(t)}$	333.938	23	278.338
$\Phi_{(t)}p_{(.)}b_{(.)}$	365.761	23	310.161
$\Phi_{(.)}p_{(.)}b_{(.)}$	367.674	13	338.762
$\Phi_{(g)}p_{(g)}b_{(g*t)}$	369.250	26	0.000
$\Phi_{(g*t)}p_{(g)}b_{(g*t)}$	428.921	46	0.000
$\Phi_{(g)}p_{(g)}b_{(g)}$	441.779	26	0.000
$\Phi_{(g*t)}p_{(g)}b_{(g)}$	477.251	46	0.000
Pleisweiler 2012			
$\Phi_{(.)}p_{(.)}b_{(t)}$	120.477	13	0.000
$\Phi_{(.)}p_{(.)}b_{(.)}$	141.108	13	0.000
$\Phi_{(t)}p_{(.)}b_{(t)}$	175.740	23	0.000
$\Phi_{(t)}p_{(.)}b_{(.)}$	194.161	23	0.000
Weyher 2011			
$\Phi_{(.)}p_{(.)}b_{(t)}$	161.694	13	126.361
$\Phi_{(.)}p_{(.)}b_{(.)}$	185.326	13	149.993
$\Phi_{(t)}p_{(.)}b_{(t)}$	191.451	23	107.383
$\Phi_{(t)}p_{(.)}b_{(.)}$	213.789	23	129.721
$\Phi_{(g)}p_{(g)}b_{(g*t)}$	234.885	26	0.000
$\Phi_{(g)}p_{(g)}b_{(g)}$	267.643	26	14.611
$\Phi_{(g*t)}p_{(g)}b_{(g*t)}$	917.698	46	0.000
$\Phi_{(g*t)}p_{(g)}b_{(g)}$	945.683	46	0.000
Weyher 2012			
$\Phi_{(.)}p_{(.)}b_{(t)}$	236.698	13	205.183
$\Phi_{(t)}p_{(.)}b_{(t)}$	256.553	23	190.839
$\Phi_{(.)}p_{(.)}b_{(.)}$	261.308	13	229.793
$\Phi_{(t)}p_{(.)}b_{(.)}$	278.639	23	212.925
$\Phi_{(g)}p_{(g)}b_{(g*t)}$	293.180	26	0.000
$\Phi_{(g)}p_{(g)}b_{(g)}$	336.916	26	0.000
$\Phi_{(g*t)}p_{(g)}b_{(g*t)}$	415.903	46	0.000
$\Phi_{(g*t)}p_{(g)}b_{(g)}$	443.412	46	0.000

5 ALLGEMEINE DISKUSSION

Der aktuell vorherrschende Klimawandel hat einen starken Einfluss auf die Ökosysteme der Erde. Als Konsequenz der sich verschiebenden Klimazonen verschiebt sich auch die Verbreitungsgrenze vieler Tier- und Pflanzenarten (Walther et al. 2002; Wilson et al. 2005; Parmesan 2006). In Zentral-Europa kann daher eine Zunahme von thermophilen Tier- und Pflanzenarten beobachtet werden.

Auch die xerothermophile Gottesanbeterin *Mantis religiosa* breitet sich in Europa nordwärts aus. Für Deutschland sind bereits seit dem Jahre 1756 (Harz 1957) erste vereinzelte Fundmeldungen von *M. religiosa* bekannt. Anhand der zeitlichen Lücken zwischen den Fundmeldungen scheint es jedoch früher, möglicherweise aufgrund unzureichend geeigneter Umweltbedingungen, keine langfristig stabilen Populationen gegeben zu haben. Erst ab dem Ende des 20. Jahrhundert sind stabile Populationen in klimatisch begünstigten Standorten in Südwestdeutschland (Baden-Württemberg; Berg et al. 2011) bekannt. Seitdem steigt die Anzahl der Fundmeldungen stetig an, sodass neben Populationen im Südwesten und Westen Deutschlands nun auch Populationen im Osten und Norden Deutschlands existieren (Berg et al. 2011; Ehrmann & Reinhardt 2011). Es wird angenommen, dass sich *M. religiosa* aufgrund der Zunahme geeigneter Habitate unter dem Klimawandel ausbreiten wird. Der Klimawandel kann die Existenz von *M. religiosa* jedoch auch gefährden, beispielsweise durch nicht auszuschließende, verstärkte Frühjahrsniederschläge (Schönwiese 2008).

Aufgrund ihrer Seltenheit und ihres gefährdeten Lebensraumes steht *M. religiosa* in Deutschland unter Schutz. Um die Art weiterhin zu schützen, ist es essentiell die Habitatbedingungen für ihre erfolgreiche Entwicklung und Etablierung in einem Gebiet zu kennen, sowie ihre Dispersionsfähigkeit und daraus schlussfolgernd ihre Extinktionswahrscheinlichkeit abschätzen zu können. In dieser Arbeit untersuchte ich folglich die Herkunft der deutschen *M. religiosa*, die Mikrohabitatpräferenz ihrer verschiedenen Lebenszyklus-Stadien als Maß für die benötigten Habitatbedingungen und das Bewegungsvermögen von adulten *M. religiosa* zur Abschätzung ihrer Dispersionsfähigkeit.

5.1 Herkunft deutscher *M. religiosa* Populationen

Um die Herkunft der deutschen *M. religiosa* Populationen zu klären, untersuchte ich die Verwandtschaft deutscher *M. religiosa* im Vergleich zu *M. religiosa* benachbarter Länder. Hierfür nutzte ich einen genetischen Untersuchungsansatz (Phylogeographie), bei dem ich Sequenzen von vier mitochondrialen Genen (COI, COII, Cyt b, ND4) untersuchte.

Die Analysen ergaben, dass sich *M. religiosa* innerhalb der untersuchten Populationen in Europa ausbreitet, was durch diverse Neu-Fundmeldungen unter anderem in der Tschechischen Republik (Janšta et al. 2008) und Polen (Liana 2007; Berg et al. 2011) sowie neuerdings auch in Lettland (Pupins et al. 2012) bestätigt wird. Außerdem zeigten meine Daten, dass die genetische Diversität der *M. religiosa* Populationen tendenziell in Richtung Deutschland abnimmt. Diese Abnahme deutet auf den Rand des Verbreitungsgebietes hin, bei dem wiederkehrende Kolonisationen und Extinktionen einen genetischen Flaschenhals-Effekt (Nei et al. 1975) auslösen. Auch der verminderte genetische Austausch zwischen Populationen, bedingt durch die Ausdünnung der Populationsdichte am Rand des Verbreitungsgebietes, ist ein Grund für die geringe genetische Diversität der Randpopulationen.

Anhand der genetischen Verwandtschaften der westlichen und östlichen deutschen *M. religiosa* Populationen zu Populationen aus Nachbarländern konnte ich zeigen, dass *M. religiosa* über zwei Richtungen nach Deutschland einwandert (zwei genetische Linien). Westliche deutsche *M. religiosa* Populationen stammen von den westeuropäischen Populationen in Frankreich ab und die östlichen deutschen *M. religiosa* Populationen stammen höchstwahrscheinlich von Populationen aus der Tschechischen Republik ab. Diese Einwanderungsrichtungen nach Deutschland sind bereits für andere Tier- und Pflanzenarten bekannt, vor allem in Bezug auf ihre postglaziale Ausbreitung (Cooper et al. 1995; Taberlet et al. 1998; Hewitt 1999). Folglich gehe ich davon aus, dass es sich bei der zurzeit beobachteten Expansion von *M. religiosa* um ihre noch anhaltende postglaziale Ausbreitung handelt, die durch die klimatische Erwärmung und der damit einhergehenden Zunahme geeigneter Habitate an ihrer nördlichen Verbreitungsgrenze begünstigt wird. Die Übereinstimmung des Verlaufes ihrer Einwanderungsrouten mit den Regionen höchster Sommertemperaturen Deutschlands belegt meine Annahme.

Der Bienenfresser *Merops apiaster* (Kinzelbach et al. 1997), der thermophile, xeromorphe Feld-Mannstreu *Eryngium campestre* (Bylebyl et al. 2008) und die Wespenspinne *Argiope bruennichi* (Kumschick et al. 2011; Krehenwinkel & Tautz 2013) wanderten im vergangenen Jahrhundert vermutlich ebenso aufgrund der klimatischen Erwärmung aus den gleichen Einwanderungsrichtungen wie *M. religiosa* entlang der wärmsten Regionen nach Deutschland ein. *Argiope bruennichi*, auch ein Lauerjäger, der sonnige, offene Standorte mit hoher Beutedichte besiedelt und häufig mit *M. religiosa* vergesellschaftet ist, besiedelte zu Beginn ihrer Einwanderung nur die wärmsten Regionen Deutschlands. Durch die Hybridisierung genetischer Linien mit unterschiedlicher geographischer Herkunft in der Mitte des letzten Jahrhunderts und durch morphologische Veränderungen hat *A. bruennichi* vermutlich eine Kältetoleranz entwickelt (Krehenwinkel & Tautz 2013), die ihr heutzutage ermöglicht das südliche Skandinavien mithilfe der kilometerweiten Windverdriftung ihrer Spinnenjungtiere (sogenannte „ballooning"; Follner & Klarenberg 1995) zu besiedeln. Im Falle einer Hybridisierung beider genetischen *M. religiosa* Linien in Deutschland vermute ich hingegen keine gesteigerte Ausbreitung, die auf eine Verbesserung ihrer Winterkältetoleranz zurück zu führen wäre, weil *M. religiosa* bereits eine hohe Winterkältetoleranz (Salt & James 1947) besitzt. Sonstige Vorhersagen über die Auswirkung einer Hybridisierung beider *M. religiosa* Linien in Deutschland sind nicht möglich, da hierfür die Kenntnis der Habitatansprüche der westeuropäischen und der zentraleuropäischen *M. religiosa* Linie erforderlich wären, die aber noch unzureichend sind.

Unter klimatischen Aspekten wird *M. religiosa* sich in Deutschland auch zukünftig weiter ausbreiten können. Dies ergaben ökologische Nischenmodelle zur aktuellen und zukünftigen Verbreitung von *M. religiosa* in Deutschland, die im Rahmen einer Fortgeschrittenenübung von Kerstin Späth erstellt wurden (unveröffentlichte Daten). Zur Erstellung der Nischenmodelle nutzte sie den Maximum Entropie Modellierungsansatz (Software MaxEnt, Version 3.3.3k; Phillips et al. 2004) und verwendete die Klimadaten von Badeck et al. (2008; TKCLIM-Datenbank), topografische Daten des digitalen Höhenmodells SRTM (DLR, Oberpfaffenhofen), Bodendaten des Landesamt Geologie und Bergbau (Modul Boden) und des Bundesamtes für Geowissenschaften und Rohstoffe, sowie Boden- und Landnutzungsdaten des CORINE 2000 Datensatzes (Level 3; http://www.corine.dfd.dlr.de). Diese Nischenmodelle zeigten, dass für *M. religiosa* sowohl unter einem nass-kalten, als auch einem trocken-warmen Klimaerwärmungsszenario in Deutschland (Badeck et al. 2008) zukünftig potentiell weitere Habitate auch in nördliche Richtung verfügbar wären. Bisher hat *M. religiosa* erst einen geringen Teil der wärmsten Regionen Deutschlands besiedelt, vermutlich bedingt sowohl durch ihre speziellen Habitatanforderungen als auch durch ihre geringe Dispersionsfähigkeit (Hideg 1994; Liana 2007).

5.2 Habitatbedingungen für *M. religiosa*

Um die Habitatbedingungen für eine erfolgreiche Etablierung von *M. religiosa* in einem Gebiet zu ermitteln, untersuchte ich die Mikrohabitatpräferenz von *M. religiosa*. Hierfür testete ich in Modellen den Effekt von Umweltparametern auf das Vorkommen von *M. religiosa* Lebenszyklus-Stadien in Mikrohabitaten. Zur Datenaufnahme führte ich in Freilanduntersuchungen Fang-Markierung-Wiederfang-Versuche mit adulten *M. religiosa* durch und erfasste rasterbasiert ihre Ootheken-Ablage, den Ootheken-Schlupf und die Imaginalhäutung. Außerdem erfasste ich rasterbasiert die Umweltparameter Temperatur, Feuchtigkeit, Substrat und Vegetationshöhe in den Mikrohabitaten der Untersuchungsflächen. Da die Luftfeuchte stets mit der Temperatur in den beiden Untersuchungsflächen korrelierte, habe ich den Einfluss der relativen Luftfeuchte nicht weiter untersucht. Zusätzlich zu den in Kapitel 3 aufgeführten Analysemethoden nutzte ich auch den Maximum Entropie Modellierungsansatz (Software MaxEnt Version 3.3.3k; Phillips et al. 2004; Kapitel 3.7.2), um den Effekt der Umweltparameter auf *M. religiosa* mit „presence-only“-Daten zu testen. Ich nutzte diesen zweiten Modellierungsansatz um die Ergebnisse mit einer weiteren statistischen Auswertemethode abzusichern, da bei Regressionsanalysen, die mit „presence-absence“-Daten arbeiten, der Einfluss der Parameter auf *M. religiosa* durch „pseudo-absences“ (Kapitel 3.7.2) falsch eingeschätzt werden kann. Zwar wurden in beiden Testansätzen unterschiedliche Modelle am besten unterstützt, doch hatten im Großen und Ganzen die gleichen Umweltbedingungen einen Einfluss auf die Lebenszyklus-Stadien von *M. religiosa*.

Meine Modellierungsergebnisse und die Ergebnisse der Habitatpräferenz zeigten, dass *M. religiosa* Imagines Mikrohabitate mit Versteck- bzw. Fluchtmöglichkeiten und mit erhöhter Temperatur sowie erhöhter Beutedichte (eigene Beobachtungen; James 1958; Berg et al. 2011) präferieren.

Für die Ei- und Larvalentwicklung spielt die Temperatur ebenfalls eine entscheidende Rolle: Meine Modellierungsergebnisse und statistische Tests belegten, dass Weibchen wärmespeichernde, wettergeschützte Substrate (beispielsweise Mauernischen) für die Oothekenablage präferieren. Dieses Verhalten wurde auch von Berg et al. 2011 für die östlichen deutschen *M. religiosa* beobachtet. So kann bereits an kühlen Frühlingstagen durch Sonneneinstrahlung dank der wärmespeichernden Eigenschaft des Substrates die Entwicklung der Eier begonnen bzw. fortgesetzt werden (Battiston & Galliani 2011; Berg et al. 2011). Auch eine vorzeitige Eientwicklung vor der Diapause, dargestellt im besten MaxEnt-Modell durch den Tag der Oothekenablage ($day_{(depos)}$; MaxEnt, Kapitel 3.7.2), beeinflusst positiv den

Oothekenschlupf. Ein schnelles Durchlaufen der Eientwicklung vor, und damit auch nach der Diapause (Berg et al. 2011) sorgt dafür, dass *M. religiosa* ihren Lebenszyklus innerhalb der kurzen Zeit zwischen Eischlupf und Tod des Adulttieres (in Deutschland von Mai bis Oktober) erfolgreich abschließen kann. Ein zu früher Eischlupf unter ungünstigen Umweltbedingungen mit Nahrungsmangel für die Larven wird durch die Abhängigkeit des Oothekenschlupfes von einer mittleren Vorwochentemperatur von mindestens 17°C vermieden (logistische Regression). Przibram (1907) fand ebenfalls die Mindesttemperatur von 17°C für die postembryonale Entwicklung von *M. religiosa*. Vergleiche der Zeitpunkte der Imaginalhäutung zwischen den Untersuchungsjahren zeigten, dass die Larvalentwicklung gleichermaßen temperaturabhängig war, da nach dem kühleren, feuchteren Frühjahr auf meinen Flächen die Adulten später entwickelt waren als im wärmeren Frühjahr, entsprechend der Beobachtungen von Liana (2007).

Da *M. religiosa* bei meinen Untersuchungen aus einer Fülle von Mikrohabitatbedingungen die für sie besten Standorte wählen konnte, stellen meine Ergebnisse nicht zwingend die tatsächlich benötigten Mindestbedingungen zum langfristigen Überleben der Populationen dar, sondern lassen nur eine Einschätzung zu, welche Umweltbedingungen von *M. religiosa* präferiert werden.

Sollten in einem Habitat vorrübergehend oder auf Dauer nicht die passenden lokalen Umweltbedingungen für eine erfolgreiche Populationsentwicklung von *M. religiosa* bestehen, droht der Population langfristig die Extinktion (Pulliam 2000). Falls Nachbarhabitate die fehlenden Bedingungen oder Strukturen für die Entwicklung von *M. religiosa* bieten, können Individuen auf diese Habitate ausweichen, sofern diese im Dispersionsradius der Art liegen und erreichbar sind. Aufgrund der räumlichen Autokorrelation der Umwelt kann es jedoch dazu kommen, dass auch auf Nachbarhabitaten nicht die passenden Umweltbedingungen herrschen, sodass die Population lokal ausstirbt. Um die Rekolonisation von *M. religiosa* bei günstigen Umweltbedingungen zu erleichtern, muss im Rahmen von Schutzmaßnahmen der Biotopverbund gefördert werden. Hierfür bedarf es des Wissens um das Bewegungsvermögen von *M. religiosa*.

5.3 Bewegungsvermögen von *M. religiosa*

Zur Untersuchung des Bewegungsvermögens von *M. religiosa* testete ich in Modellen den Einfluss von klimatischen Faktoren auf ihre Bewegungswahrscheinlichkeit und auf ihre individuelle Bewegungsdistanz. Die Modelle basieren auf den Daten der Fang-Markierung-

Wiederfang-Versuche und der Erfassung der Temperatur und der relativen Luftfeuchte aus Kapitel 3. Bei der Auswertung der Daten stellte sich jedoch heraus, dass das Bewegungsvermögen der flugfähigen männlichen *M. religiosa* möglicherweise unterschätzt wurde, sodass sich die Ergebnisse hauptsächlich auf weibliche *M. religiosa* beziehen. Zwar können Weibchen kurz nach der Imaginalhäutung auch fliegen, bevor sie aufgrund der Eiproduktion zu schwer werden, doch ist ihr selten beobachteter Flug ungerichtet und beträgt nur wenige Meter (Ehrmann 2002). Zusammen mit ihrem sonstigen geringen aktiven Bewegungsradius beschränkt sich ihre reguläre Ausbreitungsfähigkeit nur auf einige Dutzend Meter, sodass nur nahegelegene Gebiete aktiv besiedelt werden können. Aufgrund ihrer Fähigkeit zur Parthenogenese (Hideg 1996; Klass & Ehrmann 2005) sind weibliche *M. religiosa* gute Kolonisatoren (Baker 1965) und zur Abschätzung der Ausbreitung ihrer Art von größter Bedeutung.

Meine Ergebnisse zeigten, dass das Bewegungsvermögen von adulten *M. religiosa* temperaturabhängig ist, da die mittlere Vorwochentemperatur einen positiven Einfluss auf die Bewegungswahrscheinlichkeit zwischen den Erfassungstagen hatte. Solch eine Abhängigkeit der Bewegung von klimatischen Faktoren ist üblich für viele Arthropodenarten (Cammell & Knight 1992; Bale et al. 2002). Die sehr geringe Bewegungsdistanz zwischen zwei Wiederfängen von adulten *M. religiosa* hingegen scheint stark durch die Beuteverfügbarkeit bei unterschiedlichen Temperaturen beeinflusst zu sein, denn mit zunehmender Temperatur und damit einhergehender Zunahme der Beuteverfügbarkeit (Cammell & Knight 1992; Bale et al. 2002) nahm die Bewegungsdistanz des Lauerjägers *M. religiosa* ab. Bei sinkender Beuteverfügbarkeit, ausgelöst durch weiter steigende oder sinkende Temperaturen, nahm die Bewegungsdistanz von *M. religiosa* in meiner Studie wieder zu. Ehrmann (1985) und Berg et al. (2011) beschreiben ebenfalls eine sehr hohe Standorttreue von *M. religiosa* bei ausreichender Beuteverfügbarkeit. Auch für andere Lauerjäger ist ein beuteabhängiges Verhalten typisch, beispielsweise für die Gottesanbeterin *Paratenodera angustipennis,* die bei hohen Beutedichten standorttreuer ist als bei niedrigen Beutedichten (Inoue & Matsura 1983). Die Spinnenart *Argiope trifasciata* zeigt bei hoher Beutedichte ebenfalls eine geringere Bewegungsdistanz als bei niedrigen Beutedichten (Olive 1982). Der Jagdplatzwechsel der Ameisenlöwen-Larve *Myrmeleon mobilis* wurde auch durch die Beutedichte beeinflusst (Scharf & Ovadia 2006).

Dieses, von der Beutedichte abhängige Bewegungsverhalten von *M. religiosa* könnte auch die Variabilität der Bewegungsdistanzen zwischen den Studien erklären und die bisherige Unterschätzung ihrer Ausbreitungsfähigkeit begründen.

5.4 Synthese der Ergebnisse

5.4.1 Mantis religiosa und der Klimawandel

In meiner Arbeit konnte ich zeigen, dass sich *M. religiosa* in Europa und in Deutschland derzeit ausbreitet. Zwar sind die beiden, nach Deutschland einwandernden Linien von *M. religiosa* genetisch deutlich voneinander unterscheidbar, doch scheint die klimatische Erwärmung auf beide gleichermaßen einen positiven Einfluss in den letzten Jahrzehnten zu haben und ihre Ausbreitung zu begünstigen (Detzel & Ehrmann 1998; Ehrmann 2003; Liana 2007; Janšta et al. 2008; Ehrmann & Reinhardt 2011, Berg et al. 2011). Da sich sowohl die östlichen wie auch die westlichen deutschen *M. religiosa* entlang der wärmsten Regionen Deutschlands ausbreiten, gehe ich davon aus, dass die Temperaturbedingungen für die Entwicklung und Ausbreitung und damit die Temperaturpräferenzen beider Linien ähnlich sind. Beobachtungen der östlichen deutschen *M. religiosa* (Berg et al. 2011) zeigen zudem Übereinstimmungen zu den von mir beobachteten westlichen deutschen *M. religiosa* Individuen in ihrer Präferenzen für bestimmte Umweltbedingungen, beispielsweise für wärmespeichernde Substrate für die Oothekenablage oder für beutereiche Lauerplätze. Folglich beziehen sich meine nachfolgenden Interpretationen und die Vorschlägen für Schutzmaßnahmen auf beide genetischen *M. religiosa* Linien in Deutschland.

Als thermophile Art bevorzugt *M. religiosa* offene trockenwarme Landschaften mit niedriger bis halbhoher Vegetation. Diese Landschaften bieten aufgrund ihrer Beschaffenheit auch für viele Arthropoden einen Lebensraum (Franz 1931; Joern 1982; Zechner 1998), sodass der hohe Beutebedarf von *M. religiosa* gedeckt wird. Da *M. religiosa* ein euryphager, typischer Generalist ist (unveröffentlichte Daten der Diplomarbeit von Jürgen Ackermann 2013; Berg et al. 2011) wird ihr Vorkommen nicht von der Verfügbarkeit einer bestimmten Beuteart eingeschränkt, sondern ist generell durch das quantitative Angebot ihrer Beute limitiert (Berg et al. 2011).

Die Beutedichte und Beutebewegung wird durch gesteigerte Temperaturen begünstigt (Cammell & Knight 1992; Bale et al. 2002). Eine klimawandelbedingte Zunahme von Extremsommer-Ereignissen (Katz & Brown 1992) bewirkt durch ihre trocken warmen Schönwetterperioden einen Temperaturanstieg auf den Flächen, weil der Vegetationswuchs und somit der Grad der Beschattung auf den Feldern durch Trockenheit vermindert ist. Aufgrund der resultierenden hohen Beutedichte ist *M. religiosa* unter günstigen Umweltbedingungen generell sesshafter und hat eine geringere Bewegungsdistanz.

Ist den hohen Sommertemperaturen ein sehr trockenwarmes Frühjahr vorrangegangen, erreichen eine höhere Anzahl *M. religiosa* Larven das Adultstadium als unter kühleren, feuchteren Bedingungen (Hideg 1991; Niehuis & Schulte 1993; Ehrmann 2003). Zur Vermeidung von Kannibalismus, ausgelöst durch die resultierende hohe *M. religiosa* Individuendichte und ihrem Territorialverhalten, emigrieren die sonst so standorttreuen *M. religiosa* Individuen. Hierbei wird die Bewegungswahrscheinlichkeit von *M. religiosa* durch hohe Temperaturen gesteigert, sodass langwährende Extremsommer-Ereignisse wie in 2003 also neben der Populationsdichte von *M. religiosa* auch ihre Ausbreitungstendenz erhöhen (Ehrmann 2003; Liana 2007; Berg et al. 2011).

Der positive Einfluss erhöhter Temperatur auf die Art wurde auch in Nischenmodellen für *M. religiosa* in Süddeutschland sowohl unter einem trocken-warmen als auch nass-kalten Klimawandelszenario (nach Badeck et al. 2008; unveröffentlichte Daten der Diplomarbeit von Victoria Miczajka 2010) erkennbar. Hier war das Vorkommen von *M. religiosa* Populationen deutlich temperaturabhängig, insbesondere von den gemittelten Maximaltemperaturen der Monate August bis Oktober. Hohe Temperaturen und damit einhergehend hohes Nahrungsangebot für *M. religiosa* (Liana 2007) begünstigt ihr Überleben und verlängert damit ihre Reproduktionsphase und ihren Reproduktionserfolg (Berg et al. 2011). Auch eine vorzeitige Entwicklung von *M. religiosa*, ausgelöst durch eine klimawandelbedingte Verfrühung des Frühjahrs und die Verlängerung der Vegetationsperiode (Thuiller 2007; Schönwiese 2008) kann den Reproduktionserfolg der Individuen positiv beeinflussen. Eine vorzeitige Oothekenablage kann zudem die Eientwicklung in den Ootheken bereits im Frühherbst vor der winterlichen Diapause veranlassen (Niehuis et al. 2011), welches den Schlupf im nächsten Frühjahr bei günstigen klimatischen Verhältnissen vorziehen würde (Berg et al. 2011). Allerdings besteht hierbei die Gefahr, dass sich Eier von sehr früh abgelegten Ootheken spontan ohne Diapause weiterentwickeln und die Larven noch im Herbst schlüpfen (Berg et al. 2011), und bei den ersten Frösten sterben würden. Zudem wurde vereinzelt eine Austrocknung von früh abgelegten Ootheken im Herbst und einer daraus verminderten Schlupfrate im darauffolgenden Frühjahr (Liana 2007) beobachtet. Demzufolge kann nicht ausgeschlossen werden, dass die gegenwärtig beobachteten klimatischen Veränderungen neben positiven Einflüssen auf *M. religiosa* möglicherweise auch negative Auswirkungen haben können.

Im Großen und Ganzen gehe ich davon aus, dass sich die Art, ausgelöst durch hohe Abundanz (intraspezifische Konkurrenz) oder niedrige Beutedichte, in Deutschland weiter ausbreiten sollte. Auch wenn eine aktive Emigration und eine möglicherweise daraus erfolgende Kolonisation von neuen Flächen zusätzlich durch erhöhte Temperaturen gefördert werden, beträgt sie aufgrund der niedrigen Bewegungsdistanz nur mehrere Meter, sodass die Art stets der Gefahr der Extinktion unterliegt, sollten in einer Region mehrere Jahre hintereinander nicht die richtigen Bedingungen für *M. religiosa* herrschen (Brechtel et al. 1996; Liana 2007).

5.4.2 Schutzmaßnahmen für M. religiosa

Zwar zeigen meine Untersuchungen sowie zahlreiche neue Fundmeldungen, dass *M. religiosa* ihr Verbreitungsgebiet in Deutschland gegenwärtig vergrößert, doch sind ihre Vorkommen nur sehr lokal und selten. Da ihr Lebensraum in Deutschland gefährdet ist, unter anderem durch die Intensivierung der Landwirtschaft, begleitet von einer Abnahme der Brachflächen (von 2012 bis 2014 um 11,28%; Ferlmann 2014/2013) und durch den Einsatz von Pestiziden (Brechtel et al. 1996; Ehrmann & Reinhardt 2011; Berg et al. 2011), wird die Art weiterhin als gefährdet eingestuft und bedarf eines besonderen Schutzes (Bundesartenschutzverordnung 2005, Fassung vom 21.01.2013).

Erste Schutzmaßnahmen für *M. religiosa* wurden bereits von verschiedenen Autoren formuliert: Auf lokaler Ebene des Gebietsschutzes sollten Trocken- und Halbtrockenrasen erhalten bleiben und gepflegt werden, um ihren Offenlandcharakter zu bewahren und einer Verbuschung entgegenzuwirken (Brechtel 1996; Detzel & Ehrmann 1998; Zechner 1999; Schwarz-Waubke et al. 2002). Wenn es die Situation zulässt, wären solche Pflegemaßnahmen außerhalb der Vegetationsperiode und somit außerhalb der aktiven Phase des Lebenszyklus der meisten Bewohner der Fläche am schonendsten für die Fauna, da Pflegemaßnahmen immer mit Einbußen in der Abundanz der Arten der Lebensgemeinschaft einhergehen (Humbert et al. 2009).

Bei Pflegemaßnahmen während der Vegetationsperiode sollte generell auf eine Arthropoden-Fauna-verträgliche Mahd bzw. Beweidung geachtet werden. Bei den Pflegemaßnahmen auf meinen Untersuchungsflächen kurz vor bzw. während der Adultphase von *M. religiosa* konnte ich tendenziell unterschiedliche direkte Auswirkungen der Pflegemaßnahme auf die *M. religiosa* Populationen feststellen. Hierbei hatte eine kurzandauernde Mahd mit Mahdwerkzeugen einen geringeren negativen Einfluss auf die Population als eine ein-bis-zwei wöchige Beweidung durch Schafe und Ziegen. Der Schaden durch Huftritt bei der langandauernden Beweidung bewirkte neben einer stark gekürzten Vegetation auch eine langfristige Veränderung der Mikrohabitate. Auch Weyer et al. (2012) diskutieren in ihrer Arbeit verschiedene Biotop-Pflegemaßnahmen und kommen zu dem Schluss, dass sich eine intensive Beweidung durch Weidetiere während der

Vegetationsperiode negativ auf die Bodenfauna auswirken kann. Störung auf meinen Untersuchungsflächen minimierte daher nicht nur die Versteck- und Jagdhabitate von *M. religiosa*, sondern dezimierte zusätzlich stark ihre Beutepopulation (persönl. Beobachtungen; Weyer et al. 2012). Besonders die bewegungsträgeren, doch für eine Besiedlung essentiellen, weiblichen *M. religiosa* leiden verstärkt unter solchen Beeinträchtigungen. Um eine lokale Störung zu überleben, benötigt *M. religiosa* geeignete ungestörte Habitate innerhalb ihres Dispersionsradius. Bei der Mahd und speziell bei der Beweidung von einzelnen Flächen (insbesondere wenn sie stark räumlich isoliert sind) sollte dementsprechend auf eine für *M. religiosa* angemessene kleine Absteckung des zu pflegenden/ beweidenden Flächenabschnittes geachtet werden, damit eine heterogene Fläche mit gestörten (gekürzten) und ungestörten (ungekürzten) Abschnitten geschaffen wird, wie es Humbert et al. 2009 beschreiben. Dies ermöglicht *M. religiosa* und der verbleibenden Fauna ein Rückzug auf unbehandelte Flächen. Eine verringerte Frequenz der Pflegemaßnahmen pro Flächeneinheit, beispielsweise reduziert auf jedes zweite Jahr, könnte, sofern es ein geringer Vegetationswuchs auf der Fläche zulässt, auch zum Schutz von Trockenrasenarten beitragen.

Da regenreiche, kühle Frühjahre die Extinktion von westlichen wie auch östlichen deutschen *M. religiosa* Populationen bedingen können (Brechtel et al. 1996; Berg et al. 2011), werden wärmespeichernde Strukturen, an denen *M. religiosa* bevorzugt Ootheken ablegt, für die Eientwicklung in Deutschland hilfreich sein (Berg et al. 2011). Bei der Renaturierungen von Flächen sollte deshalb darauf geachtet werden, einige wärmespeichernde, eventuell anthropogen-eingebrachte Strukturen, wie Gebäudemauern auf Kasernengrundstücken oder Trockenmauern auf Weinrebflächen zu erhalten.

Neben der Verfügbarkeit bestimmter Umweltfaktoren für die Entwicklung einer Population ist auch eine ausreichend hohe genetische Diversität in ebendieser wichtig, um ihr lokales Extinktionsrisiko zu senken (Assmann et al. 2014). Meine phylogeographische Untersuchung hatte gezeigt, dass die genetische Diversität sowohl in den westlichen als auch in den östlichen deutschen *M. religiosa* Populationen extrem niedrig ist. Um die genetische Diversität zu erhöhen und damit die bestehende lokale Extinktionsgefahr (Assmann et al. 2014) von *M. religiosa* Populationen zu minimieren, sollte ihre Migration zwischen Populationen und Gebieten gefördert werden indem der Biotopverbund unter Beachtung des geringen Bewegungsradius von *M. religiosa* optimiert wird (Detzel & Ehrmann 1998). Zwar nimmt die Anzahl der klimatisch potentiell geeigneten Lebensräume für *M. religiosa* in Deutschland durch die klimatische Erwärmung zu, doch verhindert die Verbauung und Fragmentierung der Landschaft die Migration von *M. religiosa* zu ebendiesen (Fahrig 2003). Zusätzlich sollten in Korridoren geeignete Rückzugsgebiete (xerotherme Standorte) für die Art als Trittsteinhabitate erhalten bleiben (Brechtel 1996), von denen Gebiete nach einer lokalen Extinktion wiederbesiedelt werden können.

Generell kommen die Schutzmaßnahmen für *M. religiosa* auch anderen wärmeliebenden Tierarten des gleichen Habitats zugute. Wie bereits von Liana (2007) vorgeschlagen, könnte *M. religiosa* daher als Flaggschiffart für Tier- und Pflanzenarten des Halbtrocken- und Trockenrasen dienen.

5.5 Ausblick

Neben der aktiven Ausbreitung von *M. religiosa* scheint die passive Ausbreitung in Form von Verdriftung adulter fliegender Tiere durch Wind oder die Verschleppung von Individuen und Ootheken für die Verbreitung von *M. religiosa* eine große Rolle zu spielen (Brechtel et al. 1996; Liana 2007; Cungs et al. 2013). Um die Ausbreitungs- und Dispersionsfähigkeit von *M. religiosa* vollständig einschätzen zu können und damit einen Eindruck über ihre tatsächliche Extinktionsgefährdung in einem Gebiet zu bekommen, sollte die passive Ausbreitung von *M. religiosa* Lebensstadien sowie das Flugverhalten von weiblichen, und das gerichtete Flugverhalten von männlichen *M. religiosa* (Ehrmann 2002) noch eingehender untersucht werden. Auch der Einfluss der Temperatur und der relativen Luftfeuchtigkeit auf die Bewegung der Larven sollte genauer untersucht werden, da bereits Stärz et al. (2010) ein deutliches Ausbreitungsverhalten für die Larven von *M. religiosa* beobachtet haben.

Weitere Faktoren, die einen Einfluss auf die Ausbreitung und damit auf die Kolonisation und Etablierung in neuen Habitaten haben, sind z.B. die Abundanz in einer Population und die tatsächlichen (kleinstmöglichen) Habitatbedürfnisse, die eine *M. religiosa* Population zum Überleben benötigt. Diese müssten in Toleranzversuchen abgeschätzt werden.

6 ZUSAMMENFASSUNG

Klimatische Veränderungen bedingen eine Verschiebung der Verbreitungsgrenze vieler Organismen. Die Gottesanbeterin *Mantis religiosa*, eine thermophile Insektenart, breitet sich ebenfalls unter dem Klimawandel in Deutschland aus**.** Aufgrund ihrer Seltenheit und ihres eingeschränkten, gefährdeten Lebensraumes (Halbrocken- und Trockenrasen) steht sie in Deutschland unter besonderem Schutz. Um die notwendigen Informationen zur Art und ihren Habitaten für einen angemessenen Schutz zu ermitteln, rekonstruierte ich in meiner Dissertation die bisherige Ausbreitung von *M. religiosa* in Deutschland und erfasste in Freilanduntersuchungen und mit Modellierungen die Mikrohabitatpräferenz von *M. religiosa* Lebenszyklus-Stadien sowie das Bewegungsverhalten von adulten *M. religiosa*. Diese Modellierungen geben Auskünfte über die Habitatbedingungen für die erfolgreiche Etablierung von *M. religiosa* in einem Gebiet und schätzen ihr Bewegungsvermögen unter verschiedenen klimatischen Bedingungen.

Zur Rekonstruktion ihrer bisherigen Ausbreitung in Deutschland prüfte ich mithilfe von Sequenzanalysen die Verwandtschaftsbeziehungen von deutschen *M. religiosa* Individuen zu Individuen benachbarter Länder. Ich konnte zwei Immigrationsrouten von *M. religiosa* nach Deutschland identifizieren. Die westlichen deutschen *M. religiosa* Populationen stammen von französischen Populationen ab und sind vermutlich über die Burgundische Pforte und das Moseltal nach Deutschland eingewandert. Die östlichen deutschen *M. religiosa* Populationen stammen von zentraleuropäischen Populationen ab und sind vermutlich über das Elbetal eingewandert. Diese postglazialen Einwanderungsrouten liegen in Regionen mit den höchsten Sommertemperaturen Deutschlands, welches eine temperaturbedingte Ausbreitung von *M. religiosa* nahe legt. Auch anhand von statistischen Modellen konnte ich sowohl direkte als auch indirekte Einflüsse der Temperatur auf das Auftreten der Lebenszyklus-Stadien sowie auf das Vorkommen adulter *M. religiosa* in Mikrohabitaten ausfindig machen. So wurden wärmespeichernde Substrate zur Oothekenablage bevorzugt (beispielsweise Mauersteine), die die Eientwicklung von *M. religiosa* bei ungünstigen klimatischen Bedingungen unterstützt. Aus diesem Grund sollten solche Strukturen bei Renaturierungsmaßnahmen von Flächen erhalten bleiben. Der Oothekenschlupf und die Larvalentwicklung wurden ebenso durch die Temperatur beeinflusst. Die Larven schlüpften erst in einer Zeitperiode mit warmen Temperaturen, sodass ungünstige Umweltbedingungen bei der postnatalen temperaturabhängigen Entwicklung vermieden wurden. Bei der Wahl der Aufenthaltsorte der adulten *M. religiosa* konnte ich Präferenzen für Bereiche mit erhöhter Beutedichte ausmachen. Mit zunehmender Temperatur und damit einhergehender erhöhter Beutebewegung nahm das Suchverhalten und damit die Bewegungsdistanz von *M. religiosa* ab. In Schönwetterperioden mit hohen Temperaturen und ausreichender Beutedichte ist deshalb die Bewegungsdistanz des sehr standorttreuen Lauerjägers *M. religiosa* am niedrigsten. Bei ungünstigen Bedingungen, wie hoher intraspezifischer Konkurrenz, oder zu geringer Beutedichte ermöglicht die, bei warmen Temperaturen erhöhte Bewegungswahrscheinlichkeit von *M. religiosa* den Standortwechsel. Da die aktiv zurückgelegte Bewegungsdistanz von *M. religiosa* nur wenige Meter beträgt, sollte zum Schutz der Art vor lokaler Extinktion der Habitatverbund verbessert werden. Bei der Pflege von *M. religiosa* Habitaten sollte zudem auf den Schutz der Arthropoden-Fauna geachtet werden, da eine hohe Beutepopulation essentiell für *M. religiosa* ist. Dies könnte durch ein Mosaik aus gemähten/ beweideten und ungemähten/ unbeweideten Bereichen auf kleinem Raum erreicht werden.

Meine Arbeit hat gezeigt, dass *M. religiosa* zwar im Rahmen des Klimawandels nach Deutschland einwandert, sie jedoch aufgrund ihrer speziellen Bedürfnisse für ihre Entwicklung weiterhin in Deutschland gefährdet ist. Um sie weiterhin zu schützen sollten Schutzmaßnahmen an ihre ökologische Bedürfnisse angepasst werden.

7 LITERATURVERZEICHNIS

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Tagungen

2014	44th Annual Meeting of the Ecological Society of Germany: Vortrag
2013	26. Westdeutscher Entomologentag: Vortrag
2011	Klimawandel & Biodiversität - Folgen für Deutschland: Teilnahme
2011	24. Westdeutscher Entomologentag: Teilnahme
2009	Deutsche Gesellschaft für Limnologie, Jahrestagung: Vortrag
2007	Deutsche Gesellschaft für Limnologie, Jahrestagung: Vortrag
2007	100. Jahrestagung der Deutschen Zoolog. Gesellschaft: Teilnahme

Mainz, den 30.04.2015

10 ERKLÄRUNG

Hiermit versichere ich, dass ich die von mir vorgelegte Dissertation selbständig angefertigt und alle benutzten Hilfsmittel in der Arbeit angegeben habe, dass diese Dissertation nicht als Prüfungsarbeit für eine andere Prüfung eingereicht wurde und dass ich die gleiche oder Teil der Abhandlung noch nicht als Dissertation bei einer anderen Fakultät oder einem anderen Fachbereich eingereicht habe.

Mainz, den 30.04.2015

Catherine Linn