Hummeln in der Agrarlandschaft
Ressourcennutzung, Koloniewachstum und Sammelzeiten

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1 Hummeln in der Agrarlandschaft: ein Überblick

Durch die Intensivierung der Landwirtschaft wurden die Lebensräume der Agrarlandschaft in den letzten Jahrzehnten stark verändert (Matson et al. 1997, Tilman et al. 2001, Benton et al. 2003). Zerstörung und Fragmentierung von Lebensräumen stellen die wichtigsten Ursachen für den fortschreitenden Verlust der Biodiversität dar (Saunders et al. 1991, Harrison & Bruna 1999). Die zunehmende Isolation und abnehmende Größe von Habitaten führt zu einer Reduktion der Verbreitung und Häufigkeit von Arten sowie zu Veränderungen in der Struktur von Lebensgemeinschaften und Nahrungsnetzen (Tscharntke & Kruess 1999, Holt et al. 1999, Debinski & Holt 2000, Connor et al. 2000, Steffan-Dewenter & Tscharntke 2000a). Auf der Landschaftsebene können die Prozesse der Habitatfragmentierung die Landschaftsstruktur sowie biotische Interaktionen erheblich verändern und damit Ökosystemfunktionen beeinträchtigen (Kruess & Tscharntke 1994, Matthies et al. 1995, Kareiva & Wennergren 1995, Thies et al. 2003). Die meisten ökologischen Prozesse hängen nicht nur von der lokalen Ebene einzelner Habitatinseln, sondern auch von höheren räumlichen Ebenen ab. Daher sind Studien, die auf der Landschaftsebene Zusammenhänge zwischen dem räumlichen Gefüge von Landschaften und ökologischen Prozessen untersuchen, in der Ökologie von zentraler Bedeutung (Addicott et al. 1987, Turner & Gardner 1990, Bronstein 1995, Wiegand et al. 1999, Tscharntke & Brandl 2004).

Die räumliche Skalenebene, auf der Individuen die Landschaftsstruktur wahrnehmen und mit ihr interagieren, ist schwer zu identifizieren, da sie von der meist unbekannten Mobilität und den vielfältigen Interaktionen der Individuen abhängt (Wiens 1989, With & Crist 1995, Keitt et al. 1997, With et al. 1999, Tscharntke & Brandl 2004). Um die adäquate räumliche Skalenebene für Untersuchungen spezifischer ökologischer Prozesse zu bestimmen, sind deshalb Analysen mehrerer räumlicher Ebenen (*multiple*

scales) notwendig (Heads & Lawton 1983, Kareiva 1990, Wiegand et al. 1999, Steffan-Dewenter et al. 2002).

Bestäuber erfüllen aufgrund ihrer mutualistischen Interaktionen mit Pflanzen eine wichtige Funktion in Ökosystemen (Buchmann & Nabhan 1996, Daily 1997, Allen-Wardell et al. 1998, Pellmyr 2002). Diese könnte durch die fortschreitende Habitatfragmentierung und Zerstörung erheblich beeinträchtigt werden (Rathcke & Jules 1993, Bond 1995, Didham et al. 1996, Kearns et al. 1998, Johnson & Steiner 2000, Kremen et al. 2002). Studien zeigen, daß innerhalb von kleinen und isolierten Habitatinseln bzw. Pflanzenpopulationen die Diversität und Abundanz von Bestäubern reduziert ist, Blüten weniger häufig besucht werden und der Samenansatz reduziert ist (Jennersten 1988, Aizen & Feinsinger 1994, Agren 1996, Groom 1998, Steffan-Dewenter & Tscharntke 1999, Cunningham 2000). Insbesondere generalistische und mobile Bestäuber nutzen in den meisten Landschaften auch Ressourcen außerhalb der einzelnen Habitatinseln. Deshalb sollten Untersuchungen in fragmentierten Landschaften nicht nur die Habitatinseln, sondern das gesamte Landschaftsgefüge berücksichtigen (vgl. Andren 1994, Bronstein 1995, Andren et al. 1997).

Hummeln (*Bombus* spp. (Latreille), Hymenoptera: Apidae) zeichnen sich durch eine hohe Blütenstetigkeit (Fægri & van der Pijl 1971, Proctor et al. 1996), die Fähigkeit zur Thermoregulation (Heinrich 1979), eine lang andauernde Aktivität vom Frühjahr bis in den Spätsommer (Neff & Simpson 1993) und die Fähigkeit zur Vibrationsbestäubung (*buzz pollination*) (O'Toole 1993) aus. Als effiziente und weitverbreitete Bestäuber übernehmen sie eine wichtige Funktion in Agrarökosystemen (Corbet et al. 1991, Free 1993, Richards 1996, Corbet 2000, Calabuig 2000). Sie tragen wesentlich zum Erhalt der Diversität von entomophilen Blütenpflanzen bei (LaSalle & Gauld 1993, Corbet 1997, Kwak et al. 1998) und spielen bei der Bestäubung in der landwirtschaftlichen Frucht- und Samenproduktion eine entscheidende ökonomische Rolle (O'Toole 1993, Williams 1996, Kevan & Phillips 2001). Diese Ökosystemfunktion und „Serviceleistung“ könnte zukünftig durch den gravierenden Rückgang der Artenvielfalt und Abundanz von Hummeln eingeschränkt werden, der in den letzten Jahrzehnten festgestellt wurde (Williams 1982, Day 1991, Williams 1995, Bundesamt für Naturschutz 1998, Cane & Tepedino 2001, Kremen et al. 2002).

Abb. 1 Rapsfelder in einer strukturarmen Landschaft (Foto: Susanne Schiele).

Auf lokaler Ebene ist diese Reduktion vermutlich auf Veränderungen der Habitatqualität und ein geringeres Angebot an Nahrungspflanzen zurückzuführen (Fussell & Corbet 1991, Rasmont et al. 1992, Corbet 1995). Entscheidender ist wahrscheinlich die großräumige Zerstörung halbnatürlicher und natürlicher Habitatstrukturen (Banaszak 1983, 1996, Westrich 1996, Svensson et al. 2000, Walther-Hellwig & Frankl 2000b, Carvell 2002), die wichtige Nist- und Nahrungshabitate für Hummeln in der Agrarlandschaft darstellen (Fussell & Corbet 1991, Banaszak 1992, Fussell & Corbet 1992b, Corbet 1995, Meek et al. 2002, Kells & Goulson 2003). Als zusätzliches Nahrungsangebot nutzen Hummeln auch über nur kurze Zeiträume blühende Kulturpflanzen (Massentrachten), wie z.B. Raps (*Brassica napus*, Abb. 1) oder *Phacelia tanacetifolia* (Free & Ferguson 1980, Williams & Christian 1991). Die Auswirkungen der Verfügbarkeit von halbnatürlichen Habitaten und Massentrachten auf die Dichten von Hummeln werden in Kapitel 2 untersucht.

Es wurde lange Zeit angenommen, daß Hummeln Nahrung möglichst in der Nähe ihrer Nester sammeln (Brian 1957, Heinrich 1975, Kwak et al. 1991). Vermutlich wurde deshalb auch das Sammelverhalten von Hummeln hauptsächlich auf der lokalen Ebene einzelner Lebensräume untersucht (z.B. Heinrich 1976, Hodges 1985, Thomson et al. 1987, Sowig 1989, Dreisig 1995, Goulson et al. 1998). Die Ergebnisse neuerer Studien deuten jedoch an, daß Hummeln große Distanzen bei der Nahrungssuche zurücklegen (Dramstad 1996, Osborne et al. 1999), und daß ihre Sammelradien artspezifisch sind (Walther-Hellwig & Frankl 2000a, 2000b). Leider basieren diese Ergebnisse auf einer geringen Anzahl von Beobachtungen (Walther-Hellwig & Frankl 2000a, 2000b), bzw. auf Beobachtungen in einem sehr begrenzten Gebiet (700 m Radius) (Osborne et al. 1999). Somit fehlen bislang fundierte Schätzungen der artspezifischen Sammelradien von Hummeln. In Kapitel 3 werden die räumlichen Skalenebenen, auf denen die Hummelarten *B. terrestris* agg., *B. lapidarius*, *B. pascuorum* und *B. pratorum* ihre Umwelt wahrnehmen, identifiziert, um indirekt die Größe ihrer artspezifischen Sammelradien abzuleiten.

Zwischen den potentiellen Sammeldistanzen von Hummelarten und ihren artspezifischen Merkmalen könnte ein Zusammenhang bestehen: die großen Hummelarten *B. terrestris* und *B. lapidarius* entwickeln Kolonien mit zahlreichen Arbeiterinnen und haben vermutlich große Sammelradien. Für die kleineren Hummelarten *B. pascuorum* und *B. pratorum*, die deutlich kleinere Kolonien hervorbringen, werden kurze Sammeldistanzen angenommen (Alford 1975, von Hagen 1994, Walther-Hellwig & Frankl 2000b, Mauss & Schindler 2002). *B. terrestris* und *B. lapidarius* sammeln Nahrung bevorzugt in großen und dichtblühenden Pflanzenbeständen. Dagegen werden kleinere Pflanzenbestände oder vereinzelt vorkommende Nahrungspflanzen von *B. pascuorum* favorisiert (Sowig 1989, Walther-Hellwig & Frankl 2000b). Präferenzen für bestimmte Nahungspflanzen hängen mit der Rüssellänge der einzelnen Hummelarten zusammen. Die kurzrüsseligen Arten *B. terrestris*, *B. lapidarius* und *B. pratorum* bevorzugen offene Blüten mit kurzer Corolla, die langrüsselige Art *B. pascuorum* zieht Blüten mit langer Corolla vor (Teräs 1985, Dramstad & Fry 1995, Meek et al. 2002). Zusammenhänge zwischen den Sammelradien und artspezifischen Merkmalen von Hummelarten werden in Kapitel 3 diskutiert.

Hummeln haben einjährige Koloniezyklen: im Sommer begattete Königinnen überwintern und gründen im Frühjahr neue Kolonien, die nach mehreren Generationen von Arbeiterinnen im (Spät-) Sommer Geschlechtstiere (Jungköniginnen und Drohnen) hervorbringen. Im Herbst stirbt das Volk und nur die begatteten Jungköniginnen überwintern (Free & Butler 1959, Alford 1975, Prys-Jones & Corbet 1991). Für die erfolgreiche Aufzucht ihrer Brut benötigen Hummeln ein kontinuierliches Angebot an Nektar und Pollen während des gesamten Koloniezyklus (Bowers 1985, von Hagen 1994, Goulson et al. 2002a, Pelletier & McNeil 2003). Am Beispiel von *B. terrestris* wird in Kapitel 4 der Einfluß der räumlichen und zeitlichen Verfügbarkeit von Nahrungsressourcen auf die Kolonieentwicklung und den Reproduktionserfolg von Hummeln analysiert.

Theoretische Studien zeigen, daß sowohl die Sammeldistanzen als auch die Dauer von Sammelflügen durch die Ressourcenverfügbarkeit auf der Landschaftsebene beeinflußt werden können (Dukas & Edelstein-Keshet 1998, Cresswell et al. 2000). Bei der Betrachtung der Zeit- und Energiebudgets von fouragierenden Hummeln wird deutlich, daß die Kosten bzw. verminderten Gewinne, die durch lange Sammelzeiten entstehen, den Sammelerfolg stärker limitieren als die Energie, die für weite Sammelflüge aufgewendet werden muß (Beutler 1951, Heinrich 1979). Die Dauer von Sammelflügen sollte somit die Menge an eingetragener Nahrung und damit auch die Entwicklung von Hummelkolonien entscheidend beeinflussen (Bowers 1985, Pelletier & McNeil 2003). Mit automatisierten Camcordern wurde die Dauer der Sammelflüge von *B. terrestris* Arbeiterinnen aufgezeichnet. Die Auswirkungen der Ressourcenverfügbarkeit auf die Sammelzeiten und das Koloniewachstum von Hummeln werden in Kapitel 5 am Beispiel von *B. terrestris* beschrieben.

Im Rahmen der Reform der Gemeinsamen Agrarpolitik (GAP) der Europäischen Union (Agenda 2000) wurde der Ausbau von Aufgaben, die Landwirte bei der Erhaltung der Landschaft übernehmen können, als wichtige Zielvorgabe aufgenommen, um dem Verlust der Artenvielfalt von Bestäubern entgegenzuwirken (Kommission der Europäischen Gemeinschaften 1999, Institute for European Environmental Policy 2002). Eine Studie aus den Niederlanden zeigt jedoch, daß die bislang durchgeführten Agrarumweltmaßnahmen nur geringfügig zur Förderung der Bestäuber beitragen (Kleijn et al. 2001). Dies könnte durch die lokal begrenzte Umsetzung der Agrarumweltmaßnahmen auf einzelnen Schlägen begründet sein, bei der die räumliche Anordnung von Lebensräumen und Ressourcen nicht berücksichtigt wird (vgl. Grafen & Schramek 2000, BML 2000). Konzepte für zukünftige Naturschutz- und Agrarumweltmaßnahmen werden in den Kapiteln 2 bis 5 entwickelt. Dabei werden die Auswirkungen der räumlichen und zeitlichen Verfügbarkeit von Ressourcen auf die Dichten, das Sammelverhalten und das Koloniewachstum von Hummeln berücksichtigt.

Fragestellungen

In der vorliegenden Arbeit wurden die Auswirkungen der Landschaftsstruktur, d.h. der räumlichen und zeitlichen Verfügbarkeit von Ressourcen, auf die (artspezifischen) Dichten (Kapitel 2 und 3), das Koloniewachstum (Kapitel 4) und das Sammelverhalten (Kapitel 5) von Hummeln untersucht. Um die räumlichen Skalenebenen, auf denen Hummeln ihre Umgebung wahrnehmen, zu identifizieren, wurde die Ressourcenverfügbarkeit in zwölf unterschiedlich großen, konzentrisch angeordneten Landschaftsausschnitten mit Radien zwischen 250 m und 3000 m ermittelt und in Beziehung zu den untersuchten Kenngrößen gesetzt (Kapitel 2 bis 4). Folgende Fragestellungen wurden bearbeitet:

Hummeldichten und Ressourcenverfügbarkeit (Kapitel 2)

- Wirkt sich die Verfügbarkeit von unterschiedlichen Ressourcen (halbnatürliche Lebensräume und Massentrachten) auf die Dichten von Hummeln in der Agrarlandschaft aus?
- Sind halbnatürliche Lebensräume, die Nistplätze und eine kontinuierliche Versorgung mit Nahrungspflanzen bieten, von größerer Bedeutung als Massentrachten, die eine kurzzeitig verfügbare, sehr ertragreiche Nahrungsressource darstellen?
- Auf welcher räumlichen Skalenebene ist der Einfluß von Landschaftsfaktoren am stärksten, bzw. wie groß ist der von Hummeln wahrgenommene Ausschnitt einer Landschaft?

Artspezifische Sammelradien (Kapitel 3)

- Wirkt sich die Verfügbarkeit von halbnatürlichen Lebensräumen und Massentrachten unterschiedlich auf die Dichten einzelner Hummelarten aus?
- Sind die Sammelradien von Hummeln artspezifisch?
- Bestehen Zusammenhänge zwischen den Sammelradien und artspezifischen Merkmalen, wie z.B. der Körper- oder Koloniegröße, von Hummeln?

Kolonieentwicklung (Kapitel 4)

- Wird das Koloniewachstum von *B. terrestris* durch die lokale Ressourcenverfügbarkeit beeinflußt?
- Ist das Koloniewachstum von *B. terrestris* von der regionalen Verfügbarkeit halbnatürlicher Lebensräume abhängig?
- Spielt die Verfügbarkeit von ertragreichen Massentrachten zu unterschiedlichen Zeitpunkten im Koloniezyklus eine besondere Rolle?

Sammelzeiten (Kapitel 5)

- Sind die Sammelzeiten von *B. terrestris* Arbeiterinnen in Landschaften mit besonders ertragreichen Ressourcen, d.h. mit Massentrachten, kürzer als in Landschaften mit weniger ertragreichen Ressourcen, d.h. mit großen Flächenanteilen halbnatürlicher Lebensräume?
- Wirken sich unterschiedliche Sammelzeiten auf den Sammelerfolg und damit auf die Kolonieentwicklung von *B. terrestris* aus?

Untersuchungsregion und Untersuchungsgebiete

Die Untersuchungsregion liegt in der Umgebung von Göttingen (Niedersachsen) im Oberen Leinebergland zwischen dem westlichen Harzvorland und dem Weserbergland. In ihrem Zentrum befindet sich eine Muschelkalksenke mit dem Leinegraben. Das Relief ist durch flachwellige Becken und flach bis steil aufragende Bergzüge geprägt. Die Schichtstufen und Senken werden aus mesozoischen Sedimentgesteinen vom Buntsandstein bis zur Kreide gebildet. Der miozäne Vulkan des Hohen Hagen (508 m ü. NN) bildet die markanteste Erhebung (Jedicke & Jedicke 1992).

Die Region liegt im Übergangsbereich von maritimen und kontinentalem Klima der gemäßigten Breiten. Die Jahresdurchschnittstemperatur liegt bei 8,7 °C. Die höchste Monatsmitteltemperatur von 17,1 °C wird im Juli erreicht. Im Jahr fallen durchschnittlich 644,9 mm Niederschlag, von denen 81,3 mm im regenreichsten Monat Juni fallen (Wetterstation Göttingen 2004).

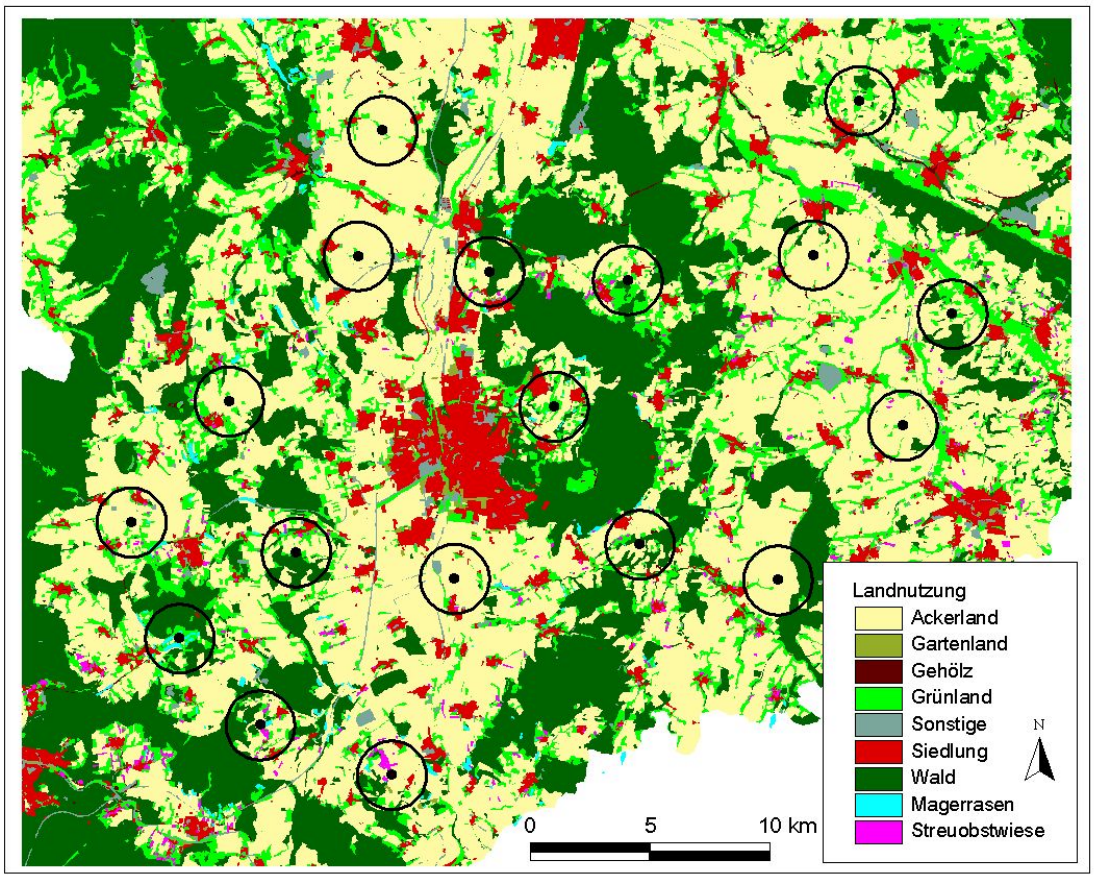

Abb. 2 Untersuchungsgebiete in der Umgebung von Göttingen (dargestellt sind die Landschaftsausschnitte mit 1500 m Radius).

In der Umgebung von Göttingen wurden 18 kreisförmige Landschaftsausschnitte mit einem Radius von 3000 m als Untersuchungsgebiete ausgewählt (Abb. 2). Die Landschaftsausschnitte bildeten einen Gradienten von strukturarmen, d.h. ackerbaulich intensiv bewirtschafteten, bis zu strukturreichen Landschaften (Abb. 3). Sie repräsentierten die für Südniedersachsen charakteristische Agrarlandschaft mit vielfältigen groß- und kleinräumigen Landnutzungstypen. Zwölf räumliche Skalenebenen wurden durch unterschiedlich große, konzentrische Teilausschnitte der Untersuchungsgebiete repräsentiert (Abb. 3).

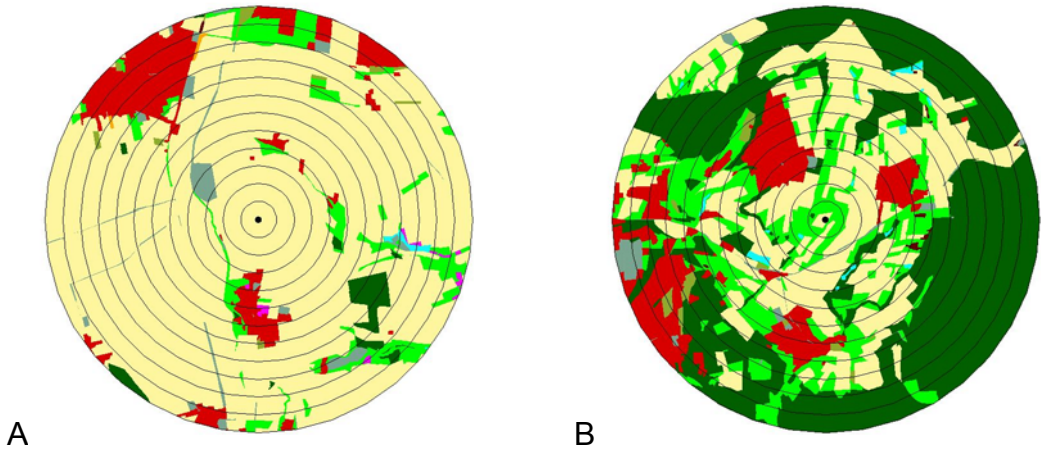

Abb. 3 Strukturarme (A) und strukturreiche (B) Landschaft. Dargestellt sind zwölf ineinander geschachtelte Ausschnitte mit Radien von 250 m bis 3000 m (räumliche Skalenebenen). Legende siehe Abb. 2.

Der experimentelle Ansatz der vorliegenden Arbeit basiert auf der Hypothese, daß lokale Prozesse und Interaktionen auf einer zentralen Untersuchungsfläche, den Einfluß der umgebenden Landschaft widerspiegeln (Tischendorf & Fahrig 2000). Deshalb wurden auf einer Brache im Zentrum der Landschaftsausschnitte alle Experimente durchgeführt und die dort ermittelten Kenngrößen (z.B. Hummeldichten) in Beziehung zur Ressourcenverfügbarkeit in den unterschiedlich großen Landschaftsausschnitten (d.h. räumlichen Skalenebenen) gesetzt.

Ergebnisse

Obwohl halbnatürliche Lebensräume aufgrund ihres kontinuierlichen Angebots an Nahrungspflanzen wichtige Ressourcen für Hummeln in der Agrarlandschaft darstellen, konnte auf keiner räumlichen Skala ein Einfluß der Verfügbarkeit von halbnatürlichen Lebensräumen auf die Dichten von Hummeln festgestellt werden. Allerdings bestand zwischen den Hummeldichten und der Verfügbarkeit von Massentrachten (hauptsächlich Raps) ein signifikant positiver Zusammenhang. Die Stärke dieses Zusammenhangs nahm mit der Größe der betrachteten Landschaftsausschnitte zu. Nur

wenn ertragreiche Massentrachten auf der Landschaftsebene (d.h. in Landschaftsausschnitten mit großen Radien) verfügbar waren, konnten signifikant erhöhte Hummeldichten festgestellt werden (Kapitel 2).

Unabhängig von den artspezifischen Sammelstrategien und Präferenzen wurden die Dichten der häufigen Hummelarten (*B. terrestris* agg., *B. lapidarius*, *B. pascuorum* und *B. pratorum*) positiv von der Verfügbarkeit von Massentrachten beeinflußt. Die stärksten Effekte der Verfügbarkeit von Massentrachten auf die Dichten von *B. terrestris* agg. bzw. *B. lapidarius* konnten auf großen räumlichen Skalenebenen, d.h. für große Landschaftsausschnitte mit 3000 m bzw. 2750 m Radius nachgewiesen werden. Offenbar nehmen *B. terrestris* agg. und *B. lapidarius*, aufgrund ihrer großen Sammelradien, große Ausschnitte ihrer Umgebung war. Die Auswirkungen der Verfügbarkeit von Massentrachten auf die Dichten von *B. pascuorum* waren auf mittleren räumlichen Skalenebenen am stärksten (Landschaftsausschnitte mit 1000 m Radius). Nur marginal signifikant wurden die Dichten von *B. pratorum* von der Verfügbarkeit von Massentrachten in Landschaftsausschnitten mit 250 m Radius beeinflußt. Zwischen der Körper- und Koloniegröße von Hummeln und ihren artspezifischen Sammelradien bestand ein Zusammenhang: je größer die Art und ihre Kolonien, desto größere Distanzen legte sie bei der Nahrungssuche zurück (Kapitel 3).

Die Verfügbarkeit von Nahrungspflanzen in der unmittelbaren Nestumgebung wirkte sich nicht auf die Biomasse der Kolonien von *B. terrestris* aus. Auch die Verfügbarkeit von halbnatürlichen Lebensräumen zeigte auf keiner räumlichen Skala und zu keinem Zeitpunkt des Experiments einen Einfluß auf das Koloniewachstum. Einen signifikant positiven Effekt auf die Biomasse der *B. terrestris* Kolonien hatte jedoch die Verfügbarkeit von Rapsfeldern in Landschaftsausschnitten mit Radien zwischen 2250 m und 3000 m. Am stärksten wirkte sich die Verfügbarkeit von Rapsfeldern in Landschaftsausschnitten mit 3000 m Radius auf die Biomasse der Kolonien in der fünften Woche des Experiments (Ende Mai) aus. Zudem bestand ein positiver Zusammenhang zwischen der Verfügbarkeit von spätblühenden Massentrachten, wie z.B. Klee (*Trifolium* spp.) oder *Phacelia*, und der Biomasse der Kolonien in der zwölften Woche des Experiments (Mitte Juli). Zu diesem Zeitpunkt benötigten die Kolonien für die erfolgreiche Aufzucht von Drohnen und Jungköniginnen ausreichend Nahrung. Die Effekte von spätblühenden Massentrachten auf das Koloniewachstum

waren am stärksten für mittlere bis große räumliche Skalen (Landschaftsausschnitte mit Radien zwischen 1000 m und 2750 m). Große, schwere *B. terrestris* Kolonien brachten junge Geschlechtstiere früher und mit größerem Erfolg hervor als kleine, leichte Kolonien (Kapitel 4).

Anhand von 870 Sammelflügen von insgesamt 220 markierten *B. terrestris* Arbeiterinnen konnte gezeigt werden, daß die Sammelflüge in Landschaftsausschnitten, in denen sehr ertragreiche Ressourcen zur Verfügung standen (*Phacelia tanacetifolia* Felder), signifikant kürzer waren als die Sammelflüge in Landschaftsausschnitten mit großen Flächenanteilen von halbnatürlichen Lebensräumen. Aufgrund der geringeren Dichten von Nahrungspflanzen in halbnatürlichen Lebensräumen benötigten Sammlerinnen dort mehr Zeit, um zwischen den einzelnen Lebensräumen und den jeweiligen Nahrungspflanzen hin und her zu pendeln. Diese zusätzlich verbrauchte Reise- bzw. Pendelzeit wirkte sich negativ auf die eingetragene Menge an Nektar und Pollen und damit auch auf das Koloniewachstum aus. Die *B. terrestris* Kolonien in Landschaftsausschnitten mit *Phacelia* Feldern nahmen signifikant mehr an Gewicht zu als die Kolonien in den Landschaftsausschnitten mit großen Flächenanteilen von halbnatürlichen Lebensräumen (Kapitel 5).

Schlußfolgerungen

Die allgemeine Annahme, daß Hummeln von blühenden Kulturpflanzen (Massentrachten), die nur über kurze Zeiträume verfügbar sind, nicht profitieren (Corbet 2000), konnte in der vorliegenden Arbeit nicht bestätigt werden. Waren Massentrachten auf der Landschaftsebene verfügbar, konnten erhöhte Hummeldichten, ein gesteigertes Koloniewachstum sowie kürzere Sammelzeiten festgestellt werden. Hummeln in der Agrarlandschaft profitieren von der Nutzung besonders ertragreicher Ressourcen, auch wenn diese nur über kurze Zeiträume zur Verfügung stehen.

Hummeln haben artspezifische Sammelradien, die im Zusammenhang mit ihrer Körpergröße stehen. Insbesondere die großen Hummelarten *B. terrestris* agg. und *B. lapidarius* scheinen ihre Umgebung auf der Landschaftsebene wahrzunehmen. Aber auch *B. pascuorum* sammelt offenbar Nahrung über beträchtliche Distanzen (1000 m).

Artspezifische Sammelradien können den Bestäubungserfolg von Kultur- und Wildpflanzen beeinflussen. Aus diesem Grund sollten die Sammelradien von Bestäubern in Risikoanalysen zum Pollen- bzw. Gentransfer zwischen genetisch veränderten Kulturpflanzen und konventionellen Kultur- bzw. verwandten Wildpflanzen berücksichtigt werden.

Unabhängig von artspezifischen Sammelstrategien und Präferenzen profitierten alle Arten von verfügbaren Massentrachten. Da hauptsächlich Raps in den Untersuchungsgebieten vorkam, nutzen anscheinend auch langrüsselige *B. pascuorum* Sammlerinnen, entgegen ihrer sonstigen Präferenz für Blüten mit langer Corolla, die massenhaft angebotenen Rapsblüten, die eine kurze Corolla haben. Felder mit blühenden Kulturpflanzen stellen aufgrund des dichten Blütenangebots, d.h. der kurzen Wege zwischen einzelnen Blüten und der meist großen Mengen an produziertem Nektar und Pollen, energetisch besonders ertragreiche Nahrungsressourcen für Hummeln dar.

Während der Kolonieentwicklung von Hummeln scheint es zwei besonders kritische Zeitpunkte im Hinblick auf die Versorgung mit Nahrung zu geben: zu Beginn der Kolonieentwicklung, wenn nur die Königin oder wenige Arbeiterinnen die Brut mit Nahrung versorgen, und gegen Ende der Kolonieentwicklung, wenn die Versorgung der heranwachsenden Geschlechtstiere gewährleistet werden muß. Zu beiden Zeitpunkten konnten signifikant positive Effekte der Verfügbarkeit von Massentrachten auf die Biomasse von *B. terrestris* Kolonien festgestellt werden. Dabei war entscheidend, daß die Massentrachten auf der Landschaftsebene verfügbar waren.

Der Reproduktionserfolg von Hummeln hing mit dem Gewicht ihrer Kolonien zusammen. Große, schwere Kolonien brachten zu einem früheren Zeitpunkt mehr Drohnen und Jungköniginnen hervor als kleine Kolonien. Das Überleben, das Wachstum und der Reproduktionserfolg von Hummelkolonien war offenbar durch die Verfügbarkeit von Nahrungsressourcen in den Untersuchungsgebieten limitiert.

Die Sammelzeiten von *B. terrestris* waren in Landschaften, in denen *Phacelia* Felder verfügbar waren, signifikant kürzer als in Landschaften mit großen Flächeanteilen von halbnatürlichen Lebensräumen. Verfügbare *Phacelia* Felder wurden als besonders ertragreiche Ressourcen wahrscheinlich systematisch ausgebeutet. Durch die kürzeren

Sammelzeiten konnten die entsprechenden Sammlerinnen größere Mengen an Nektar und Pollen pro Zeiteinheit eintragen. Die verbesserte Nahrungsversorgung wirkte sich positiv auf das Koloniewachstum und damit vermutlich auch auf den Reproduktionserfolg aus. Hummeln maximieren offenbar ihren Reproduktionserfolg, indem sie ihr Sammelverhalten an ihre Umgebung anpassen und so die Nutzung von verfügbaren Nahrungsressourcen optimieren.

In der vorliegenden Arbeit konnten keine Effekte der Verfügbarkeit von halbnatürlichen Lebensräumen auf die Dichten, das Koloniewachstum oder die Sammelzeiten von Hummeln festgestellt werden. Dies könnte u.a. durch die Intensivierung der Landwirtschaft und die damit verbundene floristische Verarmung der halbnatürlichen Habitate bedingt sein (Goulson 2003). Deshalb sollten Naturschutzmaßnahmen die floristische Zusammensetzung von halbnatürlichen Lebensräumen verbessern, so daß dort zukünftig ausreichende Mengen an ertragreichen Nahrungspflanzen für Hummeln in der Agrarlandschaft zur Verfügung stehen.

Die Ergebnisse zeigen jedoch deutlich, daß sich die Verfügbarkeit von massenhaft blühenden Kulturpflanzen positiv auf die Dichten, das Koloniewachstum und den Sammelerfolg von Hummeln in der Agrarlandschaft auswirkt. Abgesehen von der unabdingbaren Notwendigkeit alle noch bestehenden halbnatürlichen Lebensräume in der Agrarlandschaft zu erhalten, sollten deshalb die positiven Auswirkungen von Massentrachten in zukünftigen Naturschutz- und Agrarumweltmaßnahmen berücksichtigt werden.

Um vielfältige Bestäubergemeinschaften und ihren essentiellen „Bestäubungsservice“ in Agrarökosystemen zu erhalten und zu fördern, dürfen zukünftige Naturschutzmaßnahmen nicht mehr ausschließlich auf der lokalen Ebene einzelner Lebensräume umgesetzt werden. Vielmehr müssen Pläne für die Gestaltung ganzer Landschaften erarbeitet und auch zeitliche Aspekte der Verfügbarkeit von Ressourcen bedacht werden. Nur wenn die Maßnahmen auf den räumlichen Ebenen, auf denen die Bestäuber ihre Umgebung wahrnehmen, durchgeführt werden, können sie erfolgreich sein.

2 Mass flowering crops enhance pollinator densities at a landscape scale

Abstract

To counteract pollinator declines in Europe, conservation strategies traditionally focus on enhancing the local availability of semi-natural habitats, as supported by the European Union's Common Agriculture Policy. In contrast, we show that densities of bumblebees, an important pollinator group in agroecosystems, were not determined by the proportion of semi-natural habitats in agricultural landscapes. Instead, bumblebee densities were positively related to the availability of highly rewarding mass flowering crops (i.e. oilseed rape) in the landscape. In addition, mass flowering crops were only effective determinants of bumblebee densities when grown extensively at the landscape scale, but not at smaller local scales. Future conservation measures therefore should consider the importance of mass flowering crops and the need for management schemes at landscape level to sustain vital pollination services in agro-ecosystems.

Keywords: Pollination, bumblebees, *Bombus* spp., landscape-scale study, mass flowering crops, landscape structure, nesting sites, foraging habitats, conservation measures, agri-environment schemes.

Introduction

Pollination is an ecosystem service of major economic and societal value which is endangered by recent pollinator declines (Daily 1997). Destruction and fragmentation of habitats through agricultural intensification create structurally poor landscapes (Tilman et al. 2001) which adversely affect the diversity and abundance of solitary wild bees and bumblebees (Williams 1995, Kremen et al. 2002, Steffan-Dewenter et al. 2002). Furthermore, serious declines of managed honey bees have been documented (Williams et al. 1991, Watanabe 1994). However, the declines of managed honeybees and solitary wild bees may be compensated by generalist and mobile pollinators such as bumblebees (Corbet 2000, Kremen et al. 2002).

Bumblebees pollinate a wide range of wild plants and crops in agro-ecosystems (Corbet et al. 1991). For the development of their annual colonies they require a continuous supply of food plants from early spring to late summer, as usually is provided in perennial semi-natural habitats (Fussell & Corbet 1991, Corbet 1995). In addition, semi-natural habitats represent suitable nesting sites in agricultural landscapes (Svensson et al. 2000, Kells & Goulson 2003). Flowering crops are assumed to be of little value for bumblebees, because of their short flowering period (Corbet 2000). However, empirical evidence is still missing for this assumption, as far as we know.

To enhance pollinator diversity and abundance semi-natural habitats are traditionally implemented within the framework of conservation measures and agri-environment schemes (Banaszak 1992, Institute for European Environmental Policy 2002). However, pollinators benefit only marginally from the current European Union's agri-environment schemes (Kleijn et al. 2001). This deficiency of the agri-environment schemes might be due to the implementation of habitats at a local scale without considering the landscape context (With et al. 1999). Future sustainable management of European agro-ecosystems therefore will depend on the identification of key factors enhancing landscape-wide pollinator densities and appropriate spatial scales at which pollinators perceive the landscape (Kareiva & Wennergren 1995).

We tested the effects of two landscape factors possibly determining bumblebee densities in agricultural landscapes: first, the availability of nesting sites and continuously

flowering food plants (i.e. proportion of semi-natural habitats), and second the availability of short flowering, but highly rewarding mass resources (i.e. proportion of flowering crops) (Fussell & Corbet 1991, Banaszak 1992, Steffan-Dewenter et al. 2002). The influence of either landscape factor on bumblebee densities was examined from local to regional spatial scales to identify the appropriate spatial scale for the implementation of conservation schemes (Kareiva & Wennergren 1995, Steffan-Dewenter et al. 2002).

Material and methods

The study was conducted in 2001 in the vicinity of the city Göttingen (Germany) in an agricultural landscape representing typical land use types for southern Lower Saxony (Table 1). Within an area of 42 km east-west and 35 km north-south around Göttingen we selected 16 independent circular landscape sectors each with a radius of 3000 m. These landscape sectors represented a gradient of landscape complexity ranging from structurally rich to poor landscapes (Table 1). Landscape complexity did not correlate with the geographical north-south and east-west gradients.

To study scale-dependent effects of landscape complexity each circular landscape sector was subdivided into twelve nested sectors with radii from 250 m to 3000 m, representing twelve different spatial scales (Tischendorf & Fahrig 2000, Steffan-Dewenter et al. 2002). We chose the maximum scale (radius of 3000 m) larger than the reported potential foraging distances of bumblebees (Osborne et al. 1999, Walther-Hellwig & Frankl 2000b; but see below). Two landscape factors, (a) the proportion of semi-natural habitats, and (b) the proportion of flowering crops, were calculated for all twelve subsectors (i.e. spatial scales) of the 16 landscape sectors separately using Geographic Information Systems (GIS; Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany).

Table 1 Landscape characteristics for medium landscape sectors with 1500 m radius (*n* = 16).

Land use type	Mean area (%) ± 1 SE	Minimum	Maximum
Annual crops	51.01 ± 5.09	14.72	83.23
Mass flowering crops*	7.80 ± 0.87	2.55	15.12
Oilseed rape	6.95 ± 0.92	2.28	14.87
Grasslands	13.55 ± 2.06	1.86	27.42
Semi-natural habitats†	5.91 ± 0.75	1.77	13.02
Settlements	4.46 ± 0.80	0.23	14.08
Forests	17.55 ± 3.87	0.00	53.77

* ***Brassica napus*** (oilseed rape, 4 - 5), ***Trifolium* spp.** (clover, 6 - 9), *Phacelia tanacetifolia* (6 - 10), ***Vicia faba*** (field bean, 6 - 7), *Solanum tuberosum* (potato, 6 - 7), ***Sinapis arvensis*** (wild mustard, 5 - 6) and ***Helianthus annuus*** (sunflower, 7 - 9). Crops that require bee pollination for seed set or increased yields (following Free 1993) are printed in bold letters. The numbers indicate the months of the crops' main flowering period (following Oberdorfer 1994).

† fallows, calcareous grasslands, orchard meadows, woods, hedgerows, grassy banks and ditches

Bumblebee densities were recorded during 15 min observations (between July 13 and August 2, 2001) in experimental *Phacelia tanacetifolia* (Hydrophyllaceae) patches (4.5 m²), which we had established on old fallows (1.8 ha ± 0.2 ha, *n* = 16) in the centre of each landscape sector. Compared with the low cover of flowers on the fallows (4.89 % ± 0.95 %), the *Phacelia* plots were largely covered with flowers (50.5 % ± 2.2 %, minimum 33.3 %, maximum 63.3 %), and thus bumblebees were likely to be attracted (Williams & Christian 1991). Depending on weather conditions and flowering periods three to four observations were made per study site. The plots were sown between May 16 and May 22, 2001 with 3 g *Phacelia* seeds per m². To standardize nutrient supply, the plots were covered with 2 cm standard garden soil and fertilized every two weeks (approximately 80 g / m²). We used standard fertilizer with 8 % P_2O, 15 % K_2O, 6 % MgO. The area of *Phacelia* flowers covering the plot was estimated after each observation. Bumblebee densities were calculated as number of individuals per square meter *Phacelia* flowers.

Data were analysed with SPSS 11.0 for Windows (SPSS GmbH Software, Munich, Germany). In simple regression models the effects of both landscape parameters on bumblebee densities were tested individually for each spatial scale (i.e. landscape sector). For all regression models the coefficients of determination (r^2) were plotted to demonstrate the influence of spatial scale on the correlations between the landscape factors and bumblebee densities (Bowers 1985, Steffan-Dewenter et al. 2002). Arcsine square-root transformation was used to achieve normality for the proportions of semi-natural habitats (Zar 1984). Arithmetic means and standard errors of the non-transformed data are given in the text.

Results

We observed a total of 3340 non-parasitic bumblebee visits in the *Phacelia* plots during 62 15 min observations. The bumblebee density was on average 23.2 ± 1.8 bumblebee individuals / m² flowers (minimum 10.4, maximum 33.5, $n = 16$). We found seven *Bombus* species out of (presumably) nine in the region. The prevalent species were *B. terrestris* agg. (a group of *B. terrestris* and *B. lucorum*, which are difficult to distinguish in the field), *B. lapidarius* and *B. pascuorum*.

In contrast with our expectations the proportion of semi-natural habitats did not significantly influence bumblebee densities at any of the twelve spatial scales (Fig. 1; $p > 0.3$ in all cases). Even the strongest regression model, for landscape sectors with 2750 m radius, did not exhibit any evidence for a correlation between the availability of semi-natural habitats and bumblebee densities (Fig. 1a). The plotted coefficients of determination likewise did not reveal any scale-dependent pattern, suggesting that the availability of semi-natural habitats did not limit bumblebee densities on either local or regional spatial scales (Fig. 1b).

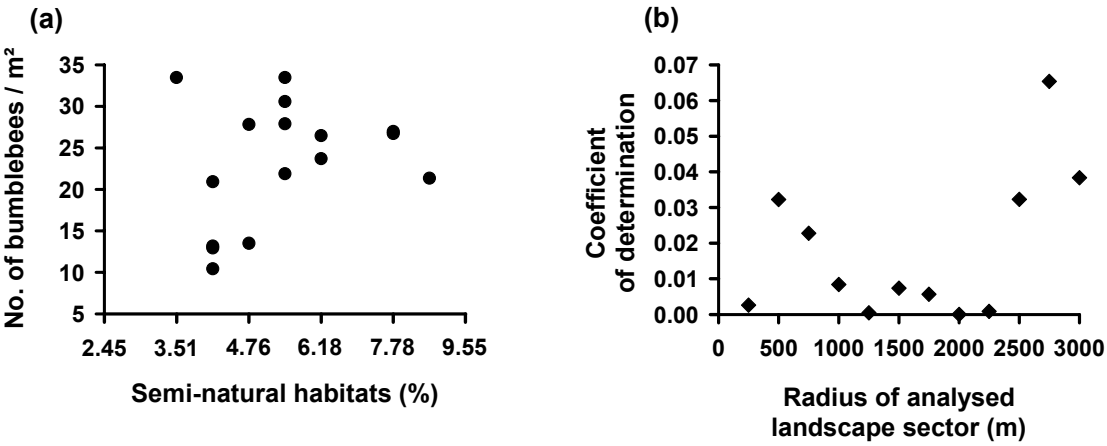

Figure 1 Effects of the proportion of semi-natural habitats on bumblebee densities. (a) Relationship between the proportion of semi-natural habitats (%) and the bumblebee density for the regression with the highest r^2 in landscape sectors with 2750 m radius ($F_{1,15} = 0.979$, $p = 0.339$, $r^2 = 0.065$). (b) r^2 values for positive simple linear regressions between the proportion of semi-natural habitats and bumblebees densities for twelve landscape sectors with 250 m – 3000 m radius. Regressions are not statistically significant ($p > 0.300$, $n = 16$).

In contrast, the availability of mass flowering crops (mainly oilseed rape (*Brassica napus*), Table 1) had strong positive effects on bumblebee densities (Fig. 2). The strongest correlation between the proportion of mass flowering crops and bumblebee densities was found for landscape sectors with 3000 m radius (Fig. 2a). The positive influence of mass flowering crops on bumblebee densities strengthened with spatial scale, as the coefficients of determination were increasing with the area of the landscape sectors (Fig. 2b). Simple linear regressions were significant for landscape sectors with more than 1250 m radius, indicating that bumblebees act at regional spatial scales, where they apparently benefit most from available mass flowering crops.

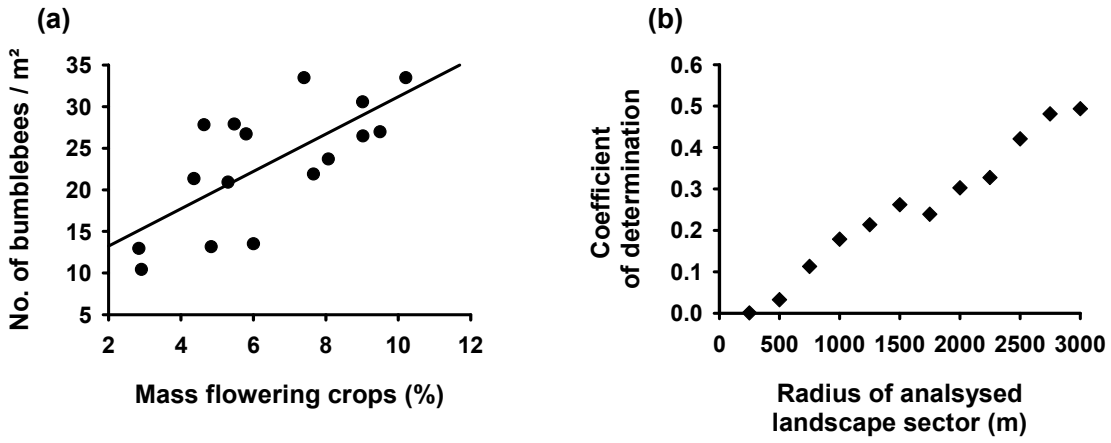

Figure 2 Scale-dependent effects of the proportion of mass flowering crops on bumblebee densities. (a) Proportion of mass flowering crops (%) in landscape sectors with 3000 m radius in relation to bumblebee densities (numbers per m² flowers; $y = 2.25\,x + 8.74$, $F_{1,15} = 13.64$, $p = 0.002$, $r^2 = 0.493$). (b) r^2 values for positive simple linear regressions between the proportion of mass flowering crops and bumblebees densities for twelve landscape sectors with 250 m – 3000 m radius. Regressions are statistically significant for landscape sectors with radii greater than 1250 m ($p < 0.050$, except for 1750 m radius: $p = 0.055$, $n = 16$).

Discussion

Since semi-natural habitats serve as nesting sites and offer a continuous as well as diverse supply of food plants throughout the season, they are considered to be of great importance for solitary wild bees and bumblebees in agricultural landscapes (Dramstad & Fry 1995, Corbet 1995, Kells & Goulson 2003). Therefore they are traditionally implemented within the framework of conservation measures and agri-environment schemes (Banaszak 1992, Kleijn et al. 2001). However, we did not find any beneficial effect of the availability of semi-natural habitats on bumblebee densities in our landscape sectors. In agricultural landscapes with at least 2 % semi-natural habitats the numbers of bumblebees were apparently not limited by the availability of nesting sites and food plants in semi-natural habitats. In contrast to bumblebees, solitary wild bees significantly profited from the availability of semi-natural habitats at small spatial scales (Steffan-Dewenter et al. 2002). This difference may be due to larger foraging distances, less restricted nesting site requirements and the more generalised use of food plants by

bumblebees (Prys-Jones & Corbet 1991, Walther-Hellwig & Frankl 2000b, Steffan-Dewenter et al. 2002, Gathmann & Tscharntke 2002). However, we cannot infer from our data, whether the rare bumblebee species, which contributed little to our results, are more dependent on semi-natural habitats than the three prevalent species. Although our study area is typical for many agricultural landscapes in central Europe, bumblebee densities might be enhanced in other landscape types characterized by much larger amounts of semi-natural or natural habitats than provided in our human-altered landscape sectors.

Deviating from the general assumption that social wild bees do not profit from annual crops such as oilseed rape because of the short flowering time (Corbet 2000), we report here great benefits in terms of bumblebee densities. The strong positive effects of the availability of mass flowering crops (mainly oilseed rape) on bumblebee densities at medium to large spatial scales indicate that mobile and generalist pollinators like bumblebees exploit mass resources over large distances. Bumblebees apparently perceive their surroundings over large distances. Furthermore, they seem to require a sufficient supply of food plants at a regional and not at a local level. The strongest correlation found at the largest spatial scale (i.e. landscape sectors with 3000 m radius) provides evidence that bumblebees have large foraging ranges and serve as efficient pollinators at a landscape level. This differs somewhat from foraging distances up to 1750 m found in recent mark-recapture experiments (Walther-Hellwig & Frankl 2000b). However, due to the exceptional high effort required to recapture individuals over large areas, mark-recapture experiments have limited ability to detect large foraging ranges. Besides that, theoretical studies indicate foraging ranges exceeding several kilometers (Dukas & Edelstein-Keshet 1998, Cresswell et al. 2000).

We found various mass flowering crops in our landscape sectors, which could provide pollen and nectar continuously until October. But only oilseed rape occurred in all landscape sectors in substantial proportions (Table 1). Hence, we consider oilseed rape to be the major mass flowering crop influencing bumblebee densities.

Oilseed rape flowers in May at the time of colony founding, when only the queen or few workers care for the brood (Alford 1975). Compared to the sparsely distributed wild plants in semi-natural habitats mass flowering crops represent energetically much more

rewarding resources (Dukas & Edelstein-Keshet 1998), which seem to be particularly beneficial for colony founding bumblebees. We assume that highly rewarding resources promote early colony growth, resulting in higher pollinator densities later in the season, when our observations took place. Since the production of reproductives is influenced by the availability of resources (Bowers 1985), population densities also might be increasing due to higher numbers of young queens founding more numerous colonies in the next spring. Nevertheless, semi-natural habitats represent important nesting sites and continuous forage resources for bumblebees (Corbet 2000) and solitary wild bees (Steffan-Dewenter et al. 2002) when no flowering crops are available.

Irrespective of the indispensable priority on the conservation of all remaining semi-natural habitats, we conclude that the importance of mass resources and the necessity to manage landscapes, and not just local habitats, should be considered in future agri-environment schemes to improve pollination services in agroecosystems. Furthermore, our results emphasize the need to broaden perspectives of ecological research to the landscape level (Kareiva & Wennergren 1995).

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3 Bumblebees experience agricultural landscapes at different spatial scales

Abstract

Bumblebees are important pollinators in agro-ecosystems. Plans for their conservation, and therewith the maintenance of a vital pollination service, require the knowledge of the spatial scales at which bumblebees perceive their surroundings, i.e. their foraging ranges. However, sound estimates of their foraging ranges are still lacking.

We investigated the effects of the landscape-wide availability of mass flowering crops on the local densities of four bumblebee species at twelve spatial scales (landscape sectors with 250 m to 3000 m radius) to indirectly identify their foraging ranges.

The densities of all bumblebee species were enhanced in landscapes with high proportions of mass flowering crops (mainly oilseed rape). We found the strongest effects for *B. terrestris* agg. and *B. lapidarius* at large spatial scales, indicating foraging ranges of 3000 m and 2750 m, respectively. The densities of *B. pascuorum* were most strongly influenced at a medium spatial scale (1000 m), and of *B. pratorum* (with marginal significance) at a small spatial scale (250 m).

Foraging range was related to body size and colony size, indicating that larger species travel over larger distances than smaller species, enabling them to build up larger colonies via a better exploitation of food resources.

We conclude that bumblebee species perceive their surroundings at species-specific spatial scales, which should be considered in conservation schemes and future studies on the driving factors of plant-pollinator interactions, including risk assessments of gene-flow from genetically modified crops. In addition, body size may indicate at which spatial scale changes in landscape structure are experienced.

Introduction

Owing to habitat loss and agricultural intensification the diversity and abundance of solitary wild bees and bumblebees (*Bombus* spp., Apidae) have declined considerably over the last decades (Williams 1982, Williams 1995, Kearns et al. 1998). Simultaneously the numbers of managed honeybees are decreasing, because of mite epidemics, high costs and low economic benefits for beekeepers (Williams et al. 1991, Watanabe 1994). These pollinator declines might have adverse implications for the pollination of wild plants and crops (Corbet et al. 1991, Kearns et al. 1998).

Bumblebees pollinate a wide range of wild flowers and crops (Corbet et al. 1991). Being widespread generalist pollinators, they might compensate the declines of solitary wild bees and honeybees to a certain degree and sustain a basic pollination service in agricultural landscapes (Corbet 2000).

For a successful completion of their colony cycle, i.e. the production of new reproductives, bumblebees require suitable nesting sites and a continuous food supply throughout the season (Bowers 1985, von Hagen 1994). In agricultural landscapes they largely use uncropped semi-natural habitats, like fallows, banks or field margins, as nesting sites (Kells & Goulson 2003) and food resources (Corbet 1995, Meek et al. 2002). Furthermore, they benefit from the availability of mass flowering crops (Westphal et al. 2003).

It has long been assumed that bumblebees forage close to their nests (Dramstad 1996), as long as food is locally abundant (Heinrich 1976). However, there is increasing evidence that bumblebees forage over large distances (Dramstad 1996, Osborne et al. 1999, Chapman et al. 2003), and that the foraging ranges of bumblebees are species-specific (Walther-Hellwig & Frankl 2000b). Hence, bumblebees presumably perceive their surroundings at landscape level. Unfortunately, sound estimates of the specific foraging distances are still missing, as most studies are limited in sample size (Walther-Hellwig & Frankl 2000b) or cover restricted areas, like harmonic radar, which is only capable to detect bees carrying transponders up to 700 m (Osborne et al. 1999). Furthermore, homing experiments were conducted that probably do not reveal the actual foraging ranges (Hedtke 1994, Goulson & Stout 2001).

The species-specific foraging ranges correspond with certain life history traits of the bumblebee species. The large species *B. terrestris* and *B. lapidarius* are assumed to forage over long distances (Walther-Hellwig & Frankl 2000b), they establish colonies with numerous workers (von Hagen 1994), and prefer the exploitation of large foraging habitats with a copious supply of food plants (Sowig 1989, Walther-Hellwig & Frankl 2000b). In contrast, the smaller *B. pascuorum* and *B. pratorum* have presumably small foraging ranges (Mauss & Schindler 2002), establish smaller colonies (von Hagen 1994), and usually forage in habitats with patchily or sparsely distributed food plants (Sowig 1989, Walther-Hellwig & Frankl 2000b). The food plant preferences of bumblebees are related to their tongue length: long tongued bumblebees (i.e. *B. pascuorum*) prefer flowers with long corollas, whereas the short tongued species (*B. terrestris* agg., *B. lapidarius* and *B. pratorum*) prefer more open shallow flowers (Teräs 1985, Sowig 1989, Dramstad & Fry 1995, Meek et al. 2002).

Considering the different foraging strategies, we assumed that bumblebee species respond to their resource environments at different spatial scales (Kareiva & Wennergren 1995, Bronstein 1995). To our knowledge little is known about the landscape characteristics that significantly influence bumblebee densities at large spatial scales (i.e. at landscape level) (Ranta & Vepsäläinen 1981, Osborne et al. 1999, Steffan-Dewenter et al. 2002). However, a recent study showed that bumblebee densities are positively related to the availability of mass flowering crops at regional spatial scales (i.e. the proportions of mass flowering crops in large landscape sectors), but not to the availability of semi-natural habitats (Westphal et al. 2003). Based on this finding, we investigated possible species-specific effects of the proportion of mass flowering crops on the densities of bumblebee species. To indirectly identify the species-specific foraging ranges multiple spatial scales, i.e. circular landscape sectors with twelve different radii, were analysed.

Materials and methods

Study region and landscape sectors

The study was carried out in 2001 within an area of 42 km east-west and 35 km north-south around the city of Göttingen (Germany). This southern Lower Saxony region comprised intensively farmed areas with annual crops (51.01 % ± 5.09 %) and grasslands (13.55 % ± 2.06 %). Between these main agricultural land use types forests, different amounts of settlements and various scattered fragments of semi-natural habitats could be found. Within the study region we selected 16 independent circular landscape sectors each with a radius of 3000 m, which represented a gradient of resource availability owing to different proportions of mass flowering crops and semi-natural habitats.

For each landscape sector the current land use was mapped using land register maps with a scale of 1:5000, which were transferred into Geographical Information Systems (GIS; Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany) for landscape analysis.

The influence of resource availability on the densities of bumblebee species was studied at multiple spatial scales. Each circular landscape sector was subdivided into twelve nested subsectors with radii from 250 m to 3000 m representing twelve spatial scales from local to landscape level. We chose the maximum scale, i.e. a radius of 3000 m, to cover a larger range than the so far reported maximum foraging distance of bumblebees (1750 m) (Walther-Hellwig & Frankl 2000b). For all twelve subsectors (i.e. spatial scales) of the 16 study sites the proportions of mass flowering crops were calculated separately using GIS (7.80 % ± 0.87 %, minimum 2.55 %, maximum 15.12 % for medium landscape sectors with 1500 m radius). Similarly, the proportions of semi-natural habitats were calculated (5.91 % ± 0.75 %, minimum 1.77 %, maximum 13.02 % for medium landscape sectors with 1500 m radius).

The landscape factor “proportion of flowering crops” summarized the amounts of oilseed rape (*Brassica napus*), clover (*Trifolium* spp.), *Phacelia tanacetifolia*, field

beans (*Vicia faba*), potatoes (*Solanum tuberosum*), mustard (*Sinapis arvensis*) and sunflowers (*Helianthus annuus*), which were available in the landscape sectors and subsectors, respectively. Oilseed rape was the most prevalent mass flowering crops in all sectors. The mass flowering crops without oilseed rape only made up 0.84 % ± 0.22 % of the medium landscape sectors with 1500 m radius. The landscape factor "proportion of semi-natural habitats" summarized the amounts of fallows, calcareous grasslands, orchard meadows, woods, hedgerows, grassy banks and ditches.

Experimental design

On an old fallow in the centre of each landscape sector a *Phacelia tanacetifolia* (Hydrophyllaceae) plot (1.5 m x 3 m) was established to implement a standardized foraging habitat with a single food plant and a uniform flower density for bumblebee observations. After removing the vegetation cover the experimental plots were dug, and *P. tanacetifolia* was sown between 16 May and 22 May 2001 with 3 g *Phacelia* seeds per m². To standardise the nutrient supply of the soil each plot was covered with 2 cm commercial garden soil prior to sowing. Commercial fertilizer with 8 % P_2O, 15 % K_2O, 6 % MgO was applied every two weeks.

P. tanacetifolia is a very attractive food plant for bumblebees (particularly for the short tongued species), as the open and shallow flowers provide great amounts of pollen and nectar (Williams & Christian 1991). Although the long tongued *B. pascuorum* generally prefers flowers with long corollas (Teräs 1985, Sowig 1989, Dramstad & Fry 1995, Meek et al. 2002), we observed substantial numbers of *B. pascuorum* foraging on *P. tanacetifolia* (see below). As *B. pascuorum* could even dominate *P. tanacetifolia* plots in mid to late summer (Williams & Christian 1991), we think that the standardized *P. tanacetifolia* plots represented an appropriate method to assess differences in bumblebee densities among landscapes.

Bumblebee observations

During the flowering-period of *P. tanacetifolia* flower-visiting non-parasitic bumblebees were recorded from 09.00 to 19.00 in suitable weather conditions. In total 62 observations (each lasting 15 min) were conducted between 13 July and 2 August 2001. The time of the day was varied for successive observations to avoid biased data. Depending on the length of the flowering period and weather conditions between three and four observations were made per study site.

Owing to differences in flower densities, the area of the plot covered by *Phacelia* flowers was estimated after each observation. On average 50.5 % ± 2.2 % of the plots were covered by *Phacelia* flowers (minimum 33.3 %, maximum 63.3 %). Taking these differences into account, the densities of the bumblebee species were calculated as numbers of flower-visiting bees per square metre *Phacelia* flowers. The densities were averaged over all observations per study site. Bumblebee species were identified in the field. Since the ecologically similar species *B. lucorum* and *B. terrestris* (von Hagen 1994) are difficult to distinguish in the field, we treated them as a group denoted as *B. terrestris* agg. Nomenclature follows Mauss (1996).

Statistical analyses

The statistical analyses were performed with SPSS 11.0 for Windows (SPSS GmbH Software, Munich, Germany). Possible effects of the proportion of semi-natural habitats and of the proportion of mass flowering crops on the mean densities of the bumblebee species were examined for all twelve spatial scales separately using simple linear regression models. We applied logarithmic transformation to the dependent variables (i.e. species-specific densities) achieving normality. As a measure for the strength of the correlations (Zar 1984), the coefficients of determination were plotted for each spatial scale (i.e. radius of landscape sectors) to reveal scale-dependent and species-specific patterns of the relationships (Bowers 1985, Steffan-Dewenter et al. 2002). Arithmetic means ± 1 SE for the non-transformed data are given in the text.

Results

Flower visiting bumblebees

In total 3340 non-parasitic bumblebee visits were observed in the *Phacelia* plots. The overall bumblebee density was on average 12.1 ± 1.2 bumblebee individuals / m² flowers (minimum 5.4, maximum 20.7, n = 16). We recorded seven non-parasitic species: *B. terrestris* agg. (1874 individuals), *B. lapidarius* (1155), *B. pascuorum* (242), *B. pratorum* (52), *B. hypnorum* (11), *B. sylvarum* (4) and *B. hortorum* (2). Since the sample size for *B. hypnorum*, *B. sylvarum* and *B. hortorum* was not large enough, we excluded these species from the statistical analyses.

Scale-dependent and species-specific effects of mass flowering crops

We did not find any significant influence of the proportion of semi-natural habitats on the densities of *B. terrestris* agg., *B. lapidarius*, *B. pascuorum* and *B. pratorum* at any spatial scale. However, the densities of all bumblebee species were significantly influenced by the availability of mass flowering crops (mainly oilseed rape) in the landscape sectors (Fig. 1a-d). In general, the relationships were positive for all spatial scales and species. For *B. terrestris* agg. we found the strongest positive effect of the proportion of mass flowering crops on the species' densities at the largest spatial scale. Great amounts of highly rewarding food resources in landscape sectors with 3000 m radius were enhancing the densities of *B. terrestris* agg. significantly (Fig. 1a). The pattern of the coefficients of determination in the scatter plot revealed that the positive effects of mass flowering crops on *B. terrestris* agg. densities were strengthening with increasing spatial scales (Fig. 1e). In agreement with the assumed large foraging ranges, this scale-dependent effect indicated that *B. terrestris* agg. workers were exploiting highly rewarding resources over large distances.

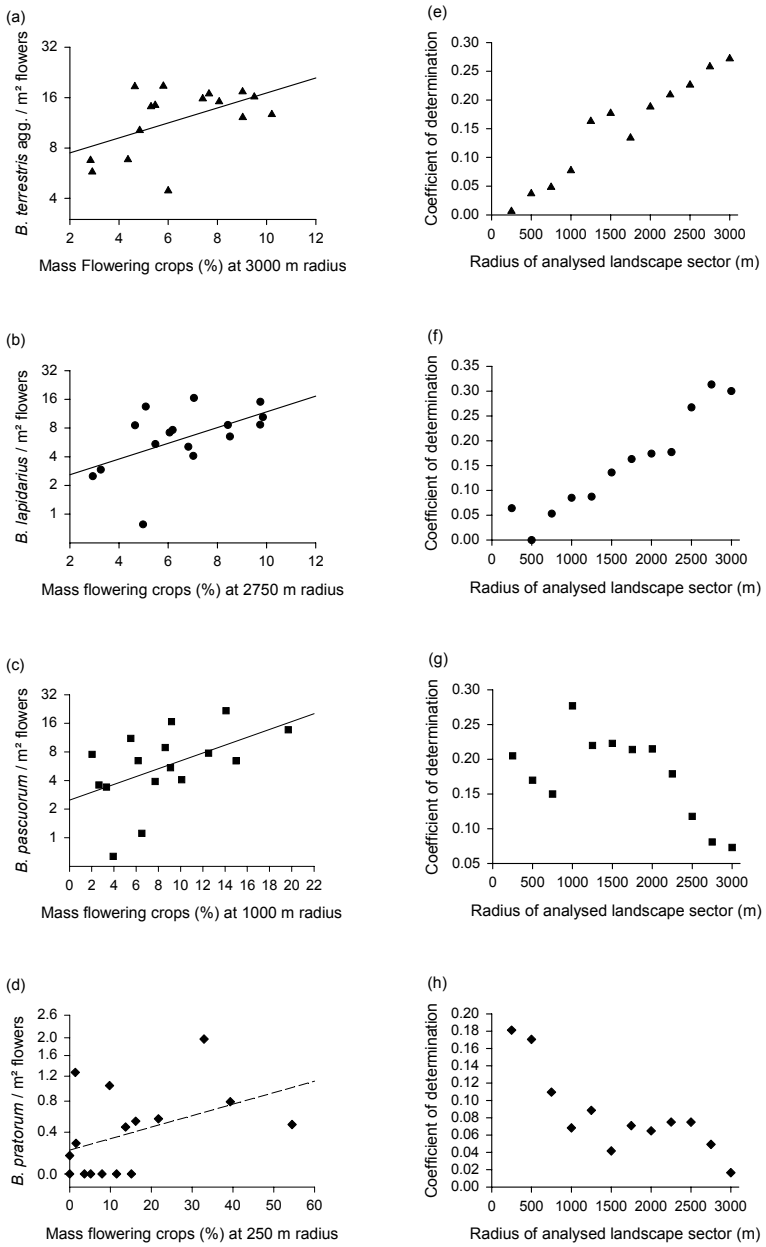

Fig. 1 Species-specific and scale-dependent effects of the availability of mass flowering crops on bumblebee densities. (a) – (d) Relationships between the proportions of mass flowering crops (%) and number of bees / m² flowers for the simple regression models with highest coefficients of determination (r^2) indicating the most influential spatial scale for each species: (a) *B. terrestris* agg. ($\log(y + 1) = 0.040\,x + 0.852$, $r^2 = 0.272$, $F_{1,15} = 5.235$, $p = 0.038$), (b) *B. lapidarius* ($\log(y + 1) = 0.066\,x + 0.438$, $r^2 = 0.313$, $F_{1,15} = 6.386$, $p = 0.024$), (c) *B. pascuorum* ($\log(y + 1) = 0.033\,x + 0.565$, $r^2 = 0.277$, $F_{1,15} = 5.371$, $p = 0.036$), and (d) *B. pratorum* ($\log(y+1) = 0.004\,x + 0.083$, $r^2 = 0.181$, $F_{1,15} = 3.099$, $p = 0.100$). (e) – (h) Coefficients of determination for simple regression models at all twelve spatial scales (i.e. radii of landscape sectors) demonstrate the species-specific patterns of scale effects for (e) *B. terrestris* agg., (f) *B. lapidarius*, (g) *B. pascuorum*, and (h) *B. pratorum*.

For *B. lapidarius* we found a similar pattern: with increasing spatial scale the positive relationships between the proportion of flowering crops and the densities of *B. lapidarius* individuals became stronger (Fig. 1f). The strongest correlation between the proportion of flowering crops and *B. lapidarius* densities occurred for landscape sectors with 2750 m radius (Fig. 1b).

The availability of highly rewarding resources was most influential on *B. pascuorum* densities in landscape sectors with 1000 m radius (Fig. 1c). The scale-dependent pattern of the plotted coefficients of determination described a plateau at medium spatial scales (Fig. 1g), indicating smaller foraging ranges than we found for *B. terrestris* agg. and *B. lapidarius*.

Even smaller foraging distances could be assumed for *B. pratorum*, as we found the strongest effect of the mass flowering crops on the species' densities at a small spatial scale (for landscape sectors with 250 m radius; Fig. 1d). Compared to the other species, this effect was weaker and only marginally significant ($p = 0.100$). The influence of the mass flowering crops on the densities of *B. pratorum* was attenuating with increasing spatial scale (Fig. 1h).

The wingspan, which strongly correlates with the size of the bumblebee species (Alford 1975, Schmid-Hempel et al. 1990), was positively related to their potential foraging distance: the larger the species the larger were their potential foraging ranges (Fig. 2). Likewise, we found a positive relation between the potential foraging ranges and the species-specific colony size. The species maintaining large colonies (*B. terrestris* agg. and *B. lapidarius*) exhibited the largest potential foraging ranges, whereas the species with smaller colonies (*B. pascuorum* and *B. pratorum*) foraged presumably over smaller distances (Fig. 3).

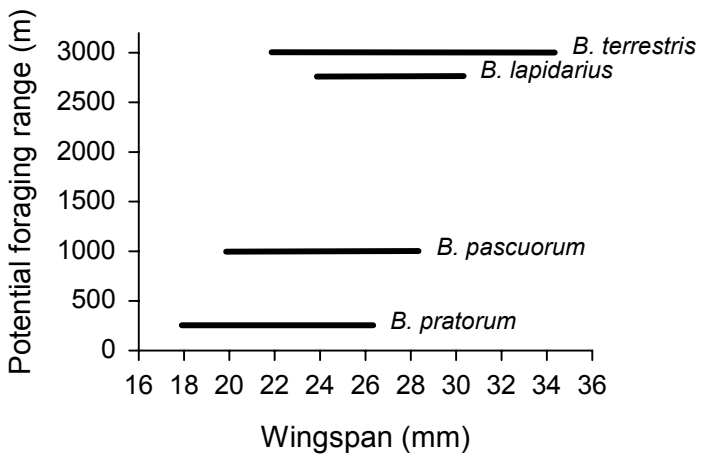

Fig. 2 Relation between the wingspan of workers (Alford 1975) and the potential foraging ranges (m) of four different bumblebee species.

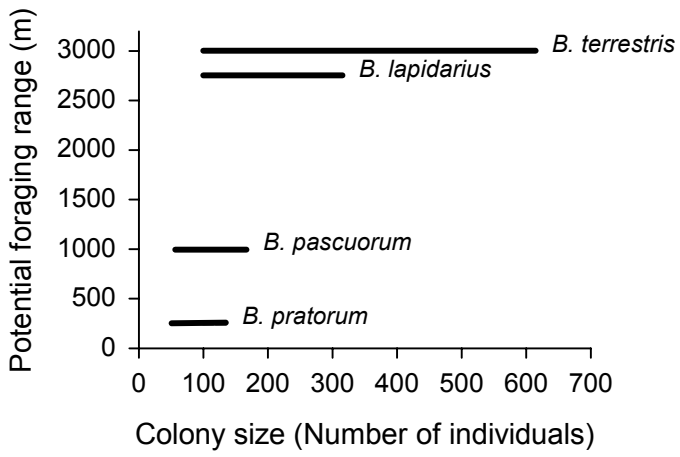

Fig. 3 Relation between the colony size (von Hagen 1994) and the potential foraging ranges (m) of four different bumblebee species.

Discussion

Species-specific foraging ranges

Our results show that the densities of bumblebee species were positively related to the availability of mass flowering crops, whereas we did not find any significant effect of the availability of semi-natural habitats on the species-specific densities of bumblebees. Most interestingly, we found species-specific patterns of the plotted coefficients of determination over the twelve spatial scales (Fig. 1d-f). The strongest correlations between mass flowering crops and the densities of *B. terrestris* agg. and *B. lapidarius* were detected for landscape sectors with 3000 m and 2750 m respectively, indicating large foraging distances for both species. The effects of the proportion of mass flowering crops on the densities of *B. terrestris* agg. became stronger with increasing size of the landscape sectors. However, for *B. lapidarius* the coefficients of determination dropped slightly at the maximum spatial scale. Since our study was restricted to landscape sectors with 3000 m radius, the spatial scale at which *B. terrestris* agg. perceives the landscape might be even larger. Regarding *B. pascuorum* the plotted coefficients of determination describe a plateau at medium spatial scales, which strongly declines at large spatial scales. Hence, the results suggest that *B. pascuorum* exploits food plants at a smaller spatial scale (i.e. within a 1000 m radius) than *B. terrestris* agg. and *B. lapidarius*. A further pattern of the plotted coefficients of determination we found for *B. pratorum*: the correlation coefficients achieve their maximum at a small spatial scale (i.e. landscape sectors with 250 m radius), and then decline continuously at the larger spatial scales.

Similarly to our study a recent mark-recapture study revealed differences in the foraging distances of *B. terrestris* agg. (maximum 1750 m), *B. lapidarius* (maximum 1500 m) and *B. muscuorum* (maximum 500 m, this species is assumed to have a similar foraging range as *B. pascuorum*) (Walther-Hellwig & Frankl 2000b). However, the possibilities to detect marked bees over large distances are limited in mark-recapture studies, since the annulus within the bees are foraging increases with the square of the distance from the nest (Osborne et al. 1999). Experiments testing the homing ability also showed that over a distance of 3 km *B. terrestris* and *B. lapidarius* returned in significantly higher

proportions than *B. pascuorum* (Hedtke 1994). Yet, the homing ability does not represent the bees' natural foraging ranges. Unfortunately, we did not find any study focussing on the foraging range of *B. pratorum*. Owing to the limitations of mark-recapture studies, harmonic radar and homing experiments, data providing sound estimates of bumblebees' actual foraging ranges are still lacking (Osborne et al. 1999). Using a multiple spatial scales analysis we provide new evidence that bumblebees have species-specific foraging ranges.

Compared to the mark-recapture study (Walther-Hellwig & Frankl 2000b), our results imply larger foraging ranges for *B. terrestris* agg., *B. lapidarius* and *B. pascuorum*. A genetic analysis of the spatial foraging patterns of *B. terrestris* and *B. pascuorum* provides further evidence that bumblebees might forage over several kilometres (Chapman et al. 2003). In addition, theoretical studies indicate that, depending on food quality and abundance, foraging flights up to several kilometres could be energetically rewarding (Dukas & Edelstein-Keshet 1998, Cresswell et al. 2000). Since mass flowering crops represent a highly rewarding resource, the bumblebee species probably decided on larger foraging distances to gather a greater reward per unit time (Heinrich 1979, Hill et al. 2001). Hence, we assume that bumblebees (like honeybees) respond to landscape structure when making foraging decisions (Steffan-Dewenter & Kuhn 2003).

The spatial scales at which bumblebees perceived their environment corresponded to their body size. We found large potential foraging ranges for the large bumblebee species *B. terrestris* agg. and *B. lapidarius*, and small potential foraging ranges for the smaller species *B. pascuorum* and *B. pratorum* (Alford 1975, von Hagen 1994) (Fig. 2). These findings are consistent with other studies that demonstrated positive correlations between the body size and foraging ranges of bee species (van Nieuwstadt & Iraheta 1996, Gathmann & Tscharntke 2002). In addition, our results provide further evidence that changes in landscape structure might affect species differentially depending on their body size (Roland & Taylor 1997).

Interestingly, the species-specific foraging ranges were also correlated with the colony size of the different species, i.e. *B. terrestris* agg. and *B. lapidarius* have larger colonies and larger potential foraging ranges than *B. pascuorum* and *B. pratorum*. (Alford 1975, von Hagen 1994, Walther-Hellwig & Frankl 2000b) (Fig. 2, Fig. 3). The ability to

forage over large distances presumably enables large bumblebee species to allocate resources much more efficiently (Spaethe & Weidenmüller 2002), and thus to translate the extra food supply in higher numbers of offspring. This assumption is supported by the finding that within a single species (*B. terrestris*) large workers collect nectar much more efficiently than small ones (Goulson et al. 2002b). In addition, the foragers of large colonies might fly further to avoid the depleted resources in the nest vicinity, and therewith minimize the intra-colony competition (Dramstad 1996, Goulson 2003).

Availability of highly rewarding resources

Food plants in semi-natural habitats, such as field margins or fallows, are generally sparsely or patchily distributed. Thus, bumblebees have to spend more time and energy collecting the same amounts of pollen and nectar than in highly rewarding mass flowering crops (Heinrich 1979, Dukas & Edelstein-Keshet 1998). We found enhanced densities of different bumblebee species in landscape sectors with high proportions of mass flowering crops. The availability of highly rewarding resources (mainly oilseed rape) apparently promoted the bumblebees' colony growth, so that we could record substantially increased bumblebee densities in the *Phacelia* plots two months after the bloom of oilseed rape ceased. Since oilseed rape was most prevalent, highly rewarding resources seemed particularly important in spring, i.e. at the time of colony founding, when only the queen or a few workers care for the brood (von Hagen 1994).

Regardless of their different foraging strategies (Teräs 1985, Sowig 1989, Walther-Hellwig & Frankl 2000b), the four dominant bumblebee species profited from mass flowering crops (Fig. 1a-d). Although *B. pascuorum* usually forages on patchily or sparsely distributed food plants with relative long corollas (Teräs 1985, Walther-Hellwig & Frankl 2000b), this species apparently exploited also the open shallow flowers of oilseed rape, which was the most predominant mass flowering crop in our landscape sectors. In contrast to *B. pascuorum*, the short-tongued species *B. terrestris* agg., *B. lapidarius* and *B. pratorum* prefer food plants with open shallow flowers (Teräs 1985, Walther-Hellwig & Frankl 2000b), like oilseed rape (Free & Ferguson 1980).

Additionally, *B. terrestris* agg. and *B. lapidarius* show a preference for mass abundant resources (Walther-Hellwig & Frankl 2000b).

Conclusions

With regard to the recent pollinator declines (Williams et al. 1991, Watanabe 1994, Kearns et al. 1998), the knowledge of landscape factors influencing pollinator densities and the spatial scales at which bumblebees perceive the landscape is important for future conservation plans and the development of vital pollination services in agricultural landscapes (Bronstein 1995, Corbet 2000, Westphal et al. 2003). Our results indicate that different bumblebee species perceive their surroundings at different spatial scales. Larger species appeared to have larger foraging ranges, resulting in larger colonies. To promote bumblebees, as important generalist pollinators, conservation schemes should take the species-specific foraging ranges into account. Species-specific foraging ranges may affect the pollination of crops and wild plant populations at landscape level, and thus should be considered in risk assessments of the pollinator-mediated gene flow from genetically modified crops to conventional crops or their wild relatives (Rieger et al. 2002). Future studies are needed to investigate, how bumblebees relate foraging decisions to resource availability at certain spatial scales.

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4 Colony growth of bumblebees is related to food availability in agricultural landscapes

Abstract

Bumblebees (*Bombus* spp.) represent an important generalist pollinator group in agro-ecosystems, although their diversity and abundance has declined considerably over the last decades. We investigated the effects of resource availability on the colony growth of *B. terrestris* from local to landscape level, to provide a scientific basis for the development of efficient conservation measures.

We selected 18 circular landscape sectors that represented a gradient in resource availability. Each sector was subdivided by twelve nested sub-sectors with radii from 250 m to 3000 m to identify the spatial scale, at which *B. terrestris* perceives the landscape, and at which conservation measures should be implemented. On a fallow in the center of each landscape sector two *B. terrestris* colonies were established on 2 May 2002. Until the end of the experiment on 19 July 2002 the biomass of the colonies and the occurrence of new reproductives was monitored.

The colony growth of *B. terrestris* was not related to the availability of local food resources (i.e. the amount of flowering plants on the fallows). Likewise, the availability of semi-natural habitats did not significantly influence the colony growth at any spatial scale or any point in time. However, the colony biomass was positively related to the percentage of oilseed rape fields, when these highly rewarding resources were available in landscape sectors with radii between 2250 m and 3000 m. The most explaining regression model occurred for landscape sectors with 3000 m radius and the colony biomass in the 5th week of the experiment, suggesting that bumblebees exploit resources at landscape level, and benefit from mass flowering crops early in the colony cycle.

In addition, we found a positive relation between the availability of late flowering crops and the colony biomass of *B. terrestris* in the 12th week of the experiment. At this point in time the colonies apparently relied on sufficient food resources to feed their reproductive offspring adequately. The relation was significant for medium to large spatial scales (between 1000 m and 2750 m radius), again indicating large foraging ranges. Furthermore, we found that large (i.e. heavy) colonies reproduced earlier and more successfully than small ones. Our results suggest that the growth, survival and reproductive success of the *B. terrestris* colonies were resource-limited in our landscape sectors.

We conclude that future conservation schemes should enhance the resource availability in agricultural landscapes, to promote divers and large bumblebee populations, and to sustain their vital pollination service. Owing to the bumblebees' large foraging ranges, conservation schemes can only enhance pollinator densities effectively when implemented at landscape level.

Keywords: Pollination, agroecosystems, mass flowering crops, semi-natural habitats, conservation, foraging, phenology of floral resources, reproductive success, agri-environment schemes.

Introduction

Bumblebees (*Bombus* spp. Latr., Apidae) pollinate a wide range of wild flowers and crops in agricultural landscapes (Corbet et al. 1991). Owing to habitat destruction and agricultural intensification the diversity and abundance of bumblebees declined considerably in North America and Europe over the last decades (Williams 1982, Williams 1995, Buchmann & Nabhan 1996, Cane & Tepedino 2001). As bumblebees are important generalist pollinators in agroecosystems (Williams 1996), their decline might have adverse effects for the pollination of wild plant populations and crops (Kearns et al. 1998, Allen-Wardell et al. 1998).

The urgency of conservation measures that effectively counteract the ongoing pollinator declines, and help to sustain a vital pollination service in agro-ecosystems has been emphasized over the last years (Pimentel et al. 1992, Daily 1997, Kremen et al. 2002). Regarding bumblebees, conservation measures that promote the implementation of semi-natural habitats are suggested (Banaszak 1992, Corbet 2000). Semi-natural habitats represent important nesting sites (Fussell & Corbet 1992b), and provide food plants throughout the season (Corbet 1995).

Bumblebees presumably have large foraging ranges, and exploit resources at landscape level (Walther-Hellwig & Frankl 2000b, Chapman et al. 2003, Westphal et al. submitted). For this reason, conservation schemes should not only consider local habitats, but also the landscape context, i.e. spatial and temporal changes in resource availability (Ranta & Vepsäläinen 1981, With et al. 1999, Westphal et al. 2003).

Landscape characteristics that might positively affect the colony growth, and therewith the general diversity and abundance of bumblebees, are largely unidentified, as far as we know. However, there is evidence that mass flowering crops enhance bumblebee densities at a landscape scale, presumably by increasing nest foundation success of hibernated queens in spring (Westphal et al. 2003). In addition, growth, survival and reproductive success of bumblebee colonies seem to be related to the (local) availability of food plants (Bowers 1985, 1986, Goulson et al. 2002a). These findings imply that the availability of different types of resources may affect bumblebee colonies at different spatial scales (Banaszak 1992). As food plants have a temporal sequence of flowering,

not only the type of resource, but also the timing of its flowering might be important (Ranta & Vepsäläinen 1981, Bronstein 1995).

Bumblebees have annual colony cycles. Hibernated queens, which have mated the previous summer, emerge in spring, locate appropriate nesting sites, and found a new colony. The queens rear the first clutch of workers solitarily. Afterwards, the first workers take over the nest duties and the foraging (Alford 1975). The colonies produce workers until some point in the colony cycle, and then switch to the production of reproductives, i.e. young queens and males (Oster & Wilson 1978, Bowers 1986). By the end of the summer the workers and males die, and only the mated young queens hibernate (von Hagen 1994).

As current agri-environment schemes proved to be little effective (Kleijn et al. 2001), we analyzed the effects of resource availability on the colony growth of *B. terrestris* L., which is a common bumblebee species in European agricultural landscapes, to provide a scientific basis for the development of efficient conservation measures for bumblebees. The possible influence of the local amount of food plants in the vicinity of bumblebee colonies, was investigated. In addition, the effects of three landscape factors, which characterized the availability of different types of resources at different points during the colony cycle, were analyzed: (a) continuously available resources, i.e. the amount of semi-natural habitats, (b) highly rewarding resources available early in the colony cycle, i.e. the amount of oilseed rape fields, and (c) highly rewarding resources available late in the colony cycle, i.e. the amount of late flowering crops. The possible effects of the three landscape factors were tested from local to regional spatial scales to identify the appropriate spatial scale for the implementation of conservation schemes (Kareiva & Wennergren 1995).

Methods

Study sites

The study was conducted in 2002 in the vicinity of the city Göttingen in southern Lower Saxony, Germany. The rural study region (42 km east-west and 35 km north-south of Göttingen) was composed of land use types, which are characteristic for central European agricultural landscapes (Table 1). Within this region we selected 18 circular landscape sectors each with a radius of 3000 m representing a gradient of landscape complexity and resource availability (Table 1). The experiment took place on an old fallow in the center of each landscape sector. The size of the fallows was on average 1.96 ha ± 0.21 (minimum 0.61 ha, maximum 3.24 ha).

The influence of resource availability on the colony growth of the bumblebee *B. terrestris* was studied at multiple spatial scales to indirectly identify the spatial scale, at which resource availability most strongly affects the colony growth, and thus foraging *B. terrestris* presumably perceive their resource environment. Twelve different spatial scales were implemented by subdividing each landscape sector into twelve nested sub-sectors with radii from 250 m to 3000 m (Tischendorf & Fahrig 2000, Steffan-Dewenter et al. 2002).

The current land use was mapped in all landscape sectors using land register maps with a scale of 1:5000, which were transferred into Geographical Information Systems (GIS; Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany). Based upon this digital land use database three landscape factors, which characterized the resource availability at different points in time during the season, were calculated for all sub-sectors (i.e. spatial scales) separately: (a) the percentage of semi-natural habitats, which represented the amount of continuously available food plants, (b) the percentage of oilseed rape, which represented a highly rewarding food supply early in the season, and (c) the percentage of late flowering crops (e.g. clover, alfalfa, *Phacelia* and sunflowers), which represented a highly rewarding resource late in the season (Table 1).

Table 1 Landscape characteristics for medium landscape sectors with 1500 m radius (*n* = 18).

	Minimum	Maximum	Mean ± 1 SE
Annual crops (%)	13.13	82.90	53.36 ± 5.03
Grasslands (%)	1.97	30.19	12.50 ± 1.94
Oilseed rape* (%)	2.42	18.70	8.64 ± 1.10
Late flowering crops† (%)	0.00	3.56	0.59 ± 0.20
Semi-natural habitats‡ (%)	1.86	14.24	6.52 ± 0.83
Settlements (%)	0.04	13.91	3.81 ± 0.71
Forests (%)	0.00	53.81	16.17 ± 3.62

* ***Brassica napus*** (oilseed rape, 4 - 5)

† ***Trifolium* spp.** (clover, 6 - 9), ***Medicago sativa*** (alfalfa, 6 – 9), *Phacelia tanacetifolia* (6 - 10), ***Vicia faba*** (field bean, 6 - 7), *Solanum tuberosum* (potato, 6 - 7), ***Sinapis arvensis*** (wild mustard, 5 - 6), ***Helianthus annuus*** (sunflower, 7 - 9) and *Nicotiana tabacum* (tobacco, 6 – 9). Crops that require bee pollination for seed set or increased yields (Free 1993) are printed in bold letters. The numbers indicate the months of the crops' main flowering period (Oberdorfer 1994).

‡ fallows, calcareous grasslands, orchard meadows, woods, hedgerows, grassy banks and ditches

Local resource availability

To characterize the local resource availability on the fallows in the center of each landscape sector the cover of flowers, which belonged to potential food plants of bumblebees, was recorded. The percentage of flowers covering each fallow was estimated during six transect walks from 13 June 2001 to 25 August 2001 (mean 4.89 % ± 0.95, minimum 0.02 %, maximum 16.56 %, *n* = 18). Based on these estimates we calculated the mean area of the fallows which was covered with flowers (m²) (mean 928 m ² ± 191, minimum 2 m², maximum 2780 m², *n* = 18).

Plate 1 Inside a *B. terrestris* colony (left), and wooden nest boxes on a fallow (right).

B. terrestris colonies

We purchased 36 *B. terrestris* colonies from STB Control, Aarbergen, Germany, which were kept in cardboard nest boxes with a transparent ventilated plastic top. According to the manufacturer, the cultured *B. terrestris* strain originated from Germany. The even aged young colonies consisted of the founding queen and approximately 15 workers. On the fallow in the center of each landscape sector two *B. terrestris* colonies were placed out on 2 and 3 May 2002.

B. terrestris usually nests below ground, yet the species is very adaptable in its choice of nesting sites (Fussell & Corbet 1992b, von Hagen 1994). To achieve a nest climate as close as possible to the natural conditions, we placed the cardboard nest boxes in special wooden boxes with a double roof covering for heat insulation (Plate 1). In addition, the wooden boxes were placed on top of four house bricks to prevent the intrusion of surface water. Bumblebees could leave or enter the nest boxes via a valve, which could be opened or closed manually.

At the beginning of the experiment the cardboard nest boxes including the brood, all workers and the founding queen were weighted before opening the entrance. Afterwards

the cardboard nest boxes were weighted in the field during daytime. Hence, the biomass of the colonies in the 5th, 8th, 10th and 12th week of the experiment might be slightly underestimated, as at the time of weighting foraging workers were absent from the nests. The (net) biomass of the colonies was calculated by subtracting the weight of an empty cardboard nest box (276 g) from the field measurements. For the statistical analysis of the effects of the local resource availability and the three landscape factors we used the mean colony biomass of the two *B. terrestris* colonies per landscape sector to avoid pseudo-replication.

The experiment was terminated 19 July 2002. At this point in time the colonies started to collapse, and by then most of them had produced reproductives, i.e. males or young queens. However, prior to the end of the experiment five colonies had died already, they were collected from the field in the 10th week. In the 12th week we collected the remaining 31 colonies from the field and placed the nest boxes in a –25°C freezer to kill and preserve them for subsequent dissection. For all 36 colonies the total number of empty brood cells, the weight of the remaining brood (i.e. the larvae and pupae), as well as the numbers of young queens, males and workers, which remained in the frozen nests, were recorded. Unfortunately, it was not possible to distinguish the brood cells of workers, males or queens unambiguously.

During weekly inspections of the colonies, which we started in the 8th week of the experiment, the first appearance of reproductives was recorded. Throughout the entire experiment we controlled the colonies for invading cuckoo bumblebees (*Psithyrus* spp.) and wax moths (*Aphomia sociella*), which are natural enemies of bumblebees that could seriously damage their nests (von Hagen 1994). However, we did not find any *Psithyrus* spp. or wax moth larvae in the nests.

Statistical analysis

Data were analyzed with SPSS 11.0 for Windows (SPSS GmbH Software, Munich, Germany). Differences between the biomass of the colonies that did not reproduce, the colonies that produced only males, and the ones that produced both young queens and males were inspected by a one-way analysis of variance (ANOVA) and Scheffé's test

(Zar 1984). The relationship between the timing of reproduction (i.e. the first occurrence of males or young queens in the colonies) and the colony biomass was analyzed using Spearman's rank correlation procedure (Spearman' rho r_S is given in the text) (Zar 1984). Regarding the reproductive success, we focused on the biomass of the colonies in the 10th week, since this was the point in time when all except for three nests achieved their maximum weight.

Simple linear regression models were used to analyze the influence of the local resource availability on the colony biomass at different points in time during the colony cycle. The effects of the three landscape factors on the colony biomass were tested individually for each spatial scale (i.e. landscape sector) with simple linear regression models, too. To demonstrate the influence of the spatial scale on the relationships between the landscape factors and the colony biomass, we plotted the coefficients of determination (r^2) for all regression models (Bowers 1985, Steffan-Dewenter et al. 2002).

We are aware of the problem that without Bonferroni adjusts the performance of multiple statistical tests might cause spurious results (Rice 1989). However, using multiple statistical tests is the only way to identify the landscape factors and spatial scales that might affect the colony growth. We are confident that the distinct pattern of our significant results did not occur by chance, as according to the Bernoulli equation the chance of eight significant regressions out of twelve would be $p < 0.0001$ (Moran 2003).

Logarithmic transformation was applied to the biomass data, the data characterizing the local resource availability (area covered by flowers) were square root transformed, and the proportional data were arcsine-square root transformed to achieve normality (Zar 1984). Arithmetic means and one standard error of the non-transformed data are given in the text.

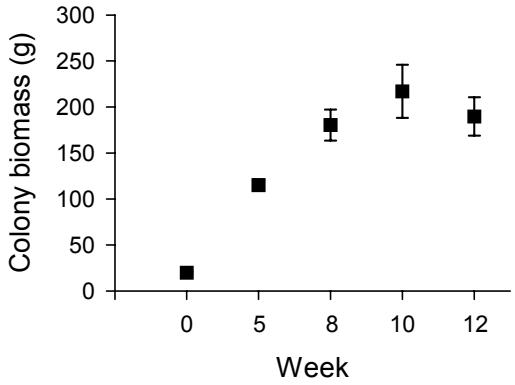

Fig. 1 Seasonal development of the *B. terrestris* colonies. The mean colony biomass ± 1 SE is given for the different measurements throughout the experiment (until the 10th week: $n = 36$, in the 12th week: $n = 31$).

Results

Colony development and reproductive success

At the beginning of the experiment the 36 *B. terrestris* colonies weighted on average 19.83 g ± 1.08. The colonies gained biomass fairly quickly. By the 5th week of the experiment their mean biomass was approximately six times larger than at the beginning. The colonies continued to grow until the 10th week, when most of them achieved their maximum weight. By the end of the experiment the mean colony biomass was slightly decreasing (Fig. 1), indicating that most nests were finishing their colony cycle. However, in some nests we found considerable amounts of brood (i.e. larvae and pupae), which did not hatch until the termination of the experiment (Table 2).

Some *B. terrestris* colonies produced substantial numbers of offspring, as the mean number of 263 empty brood cells per colony and the maximum number of 147 workers, which were remaining in one colony, indicate. In addition, we found fairly high

Table 2 Characteristics of the dissected *B. terrestris* colonies.

	Minimum	Maximum	Mean ± SE
Biomass of remaining larvae and pupae (g)	5	119	35.15 ± 4.92
Total number of empty brood cells	64	586	262.58 ± 22.56
Number of remaining young queens	0	53	3.11 ± 1.67
Number of remaining males	0	102	14.50 ± 3.37
Number of remaining workers	1	147	18.61 ± 4.53

Notes: The biomass of remaining larvae and pupae, the numbers of empty brood cells and remaining bumblebees in the nests refer to what we found in the nest boxes after collecting them from the field ($n = 36$).

maximum numbers of remaining young queens (53) and males (102) in single colonies (Table 2). The numbers of workers, young queens and males, which were remaining in the nest boxes by the end of the experiment, do not represent the numbers of reproductives or workers that were actually produced in the colonies. Yet, they give a rough estimate of the numbers of individuals that might occur in *B. terrestris* colonies at some point during their colony cycle.

The production of reproductives (i.e. young queens or males) was related to the colony biomass in the 10th week of the experiment. We found significant differences between the biomass of colonies that did not reproduce, colonies that produced only males, and colonies that produced both young queens and males (ANOVA: $F_{2,33} = 10.97$, $p < 0.001$, Fig. 2). Furthermore, the timing of reproduction was significantly correlated with the biomass of the colonies that successfully produced only males or both young queens and males (Fig. 3). Heavy colonies started to reproduce earlier than the colonies with less biomass. We are confident that none of the colonies, which did not reproduce until the end of the experiment (19 July 2002), would have started to produce males or queens later on in the season, because these colonies were not producing any new brood cells during the last weeks of the experiment.

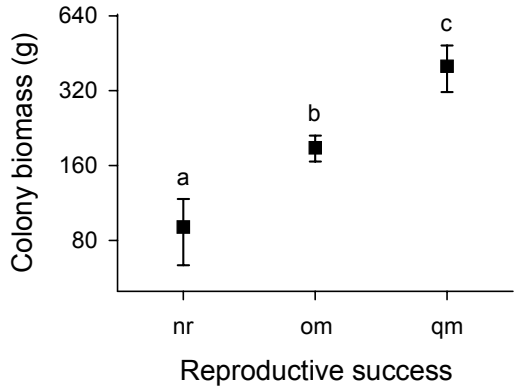

Fig. 2 Colony biomass and reproductive success. Mean Biomass ± 1 SE of the *B. terrestris* colonies that did not reproduce (nr, $n = 7$), the colonies that produced only males (om, $n = 21$), and the colonies that produced both young queens and males (qm, $n = 8$). Different letters indicate significant differences between the means (Scheffé's test, $p < 0.050$). Biomass is given for the 10th week of the experiment.

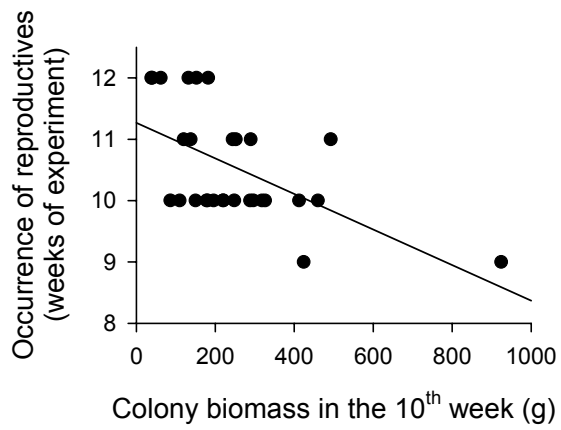

Fig. 3 Relationship between the timing of reproduction and the colony biomass. The point in time when the first reproductives (i.e. males or young queens) were observed in the colonies was negatively correlated with the colony biomass in the 10th week of the experiment ($r_S = -0.541$, $p < 0.002$, $n = 29$).

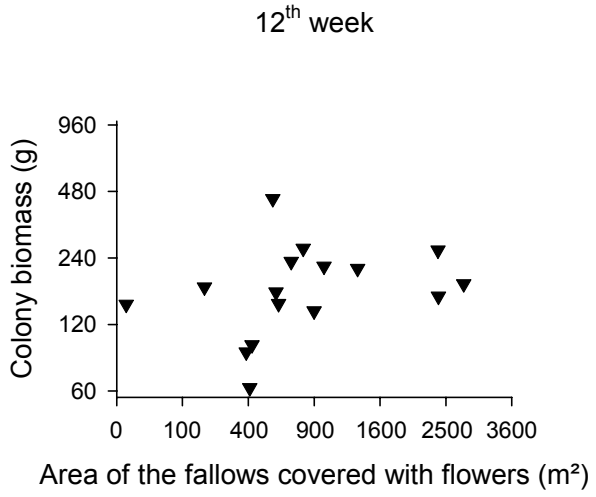

Fig. 4 Relationship between the local resource availability, i.e. the mean area of the fallows which was covered with flowers (m²), and the colony biomass of *B. terrestris* in the 12th week of the experiment ($F_{1,14} = 1.37$, $p = 0.261$, $r^2 = 0.089$).

Influence of local and regional resource availability on the colony biomass

The local resource availability, i.e. the area of the fallows, which was covered with flowers (m²), did not affect the colony growth at any point in time. We found the most explaining, but not significant regression model for the colony biomass in the 12th week (Fig. 4). Likewise, we did not find any significant effect of the percentage of semi-natural habitats on the colony biomass at any spatial scale or at any point in time ($p > 0.150$, $n = 18$).

Regarding the availability of early flowering crops, we found a positive but statistically not significant trend between the percentage of oilseed rape in landscape sectors with 3000 m radius and the colony biomass in the 5th week ($F_{1,16} = 2.39$, $p = 0.142$, $r^2 = 0.130$). However, the scatter plot of the data revealed an obvious outliner, i.e. heavy colonies (153 g mean biomass) in a landscape with a very low availability of oilseed rape (3.12 % oilseed rape fields in the landscape sector with 3000 m radius). Generally, this particular landscape was characterized by great amounts of grasslands (e.g. 30 % for landscape sectors with 1500 m radius; Table 1). Therefore, we assume that this outlier reflects the beneficial effects of copiously available dandelion (*Taraxacum officinale*), which was flowering in the grasslands during May. The outlier had a

profound influence on the slope and correlation coefficient of the regression, but did presumably not reflect the effects of the availability of oilseed rape on the colony biomass. For this reason, we decided to omit the outlier and to refit the regression models for all spatial scales and points in time (Krzanowski 1998).

Subsequently, we found positive effects of the availability of oilseed rape on the colony biomass in the 5th and 8th week of the experiment ($p < 0.050$). Consistently with the above mentioned trend, the most explaining regression model occurred for landscape sectors with 3000 m radius and the colony biomass in the 5th week, at this point in time the flowering of oilseed rape had just finished (Fig. 5A). The plotted coefficients of determination show that the colony biomass was most strongly affected, when oilseed rape fields were available at landscape level, i.e. in landscape sectors with 3000 m radius (Fig. 5B). Regarding the colony biomass in the 8th week, we found a similar, yet weaker pattern: the only significant correlation between the colonies' biomass and the percentage of oilseed rape fields occurred for landscape sectors with 3000 m radius ($F_{1,15} = 5.089$, $p = 0.039$, $r^2 = 0.253$). Again, the coefficients of determination were generally increasing with spatial scale, but they achieved much lower values than in the regression models for the colony biomass in the 5th week (Fig. 5B).

In addition, the colony biomass in the 12th week of the experiment was significantly affected by the availability of late flowering crops (Fig. 6A). This beneficial effect occurred only for the colony biomass in the 12th week of the experiment, suggesting that highly rewarding resources were particularly valuable for the colonies in mid July. We found the strongest correlation between the colony biomass and the percentage of late flowering crops for landscape sectors with 1500 m (Fig. 6A). The plotted coefficients of determination revealed a scale-dependent pattern of this effect: the influence of the availability of late flowering crops was strongest and significant for landscape sectors with radii between 1000 m and 2750 m. Thus, the coefficients of determination describe a plateau, which drops of at the ends, i.e. at the smallest and largest spatial scales (Fig. 6B).

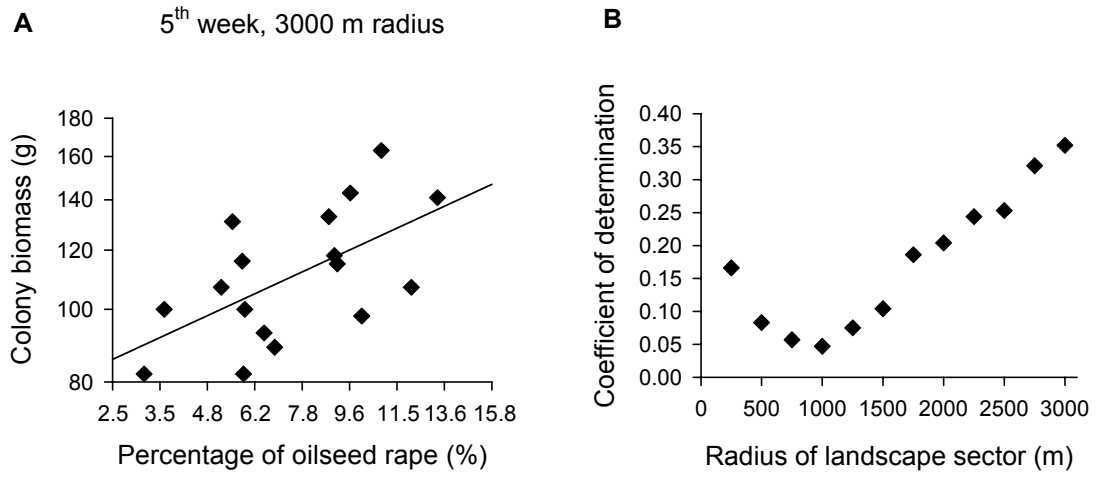

Fig. 5 Effects of the availability of early flowering crops on the colony biomass of *B. terrestris*. (A) Simple linear regression model with the highest coefficient of determination: relationship between the percentage of oilseed rape in landscape sectors with 3000 m radius and the colony biomass in the 5th week of the experiment ($F_{1,15} = 8.16$, $p = 0.012$, $r^2 = 0.352$). (B) Coefficients of determination for simple linear regressions between the percentage of oilseed rape and the colony biomass in the 5th week for 12 landscape sectors with 250 m – 3000 m radius. The regressions are statistically significant for landscape sectors with radii between 2250 m and 3000 m ($p < 0.050$, $n = 17$).

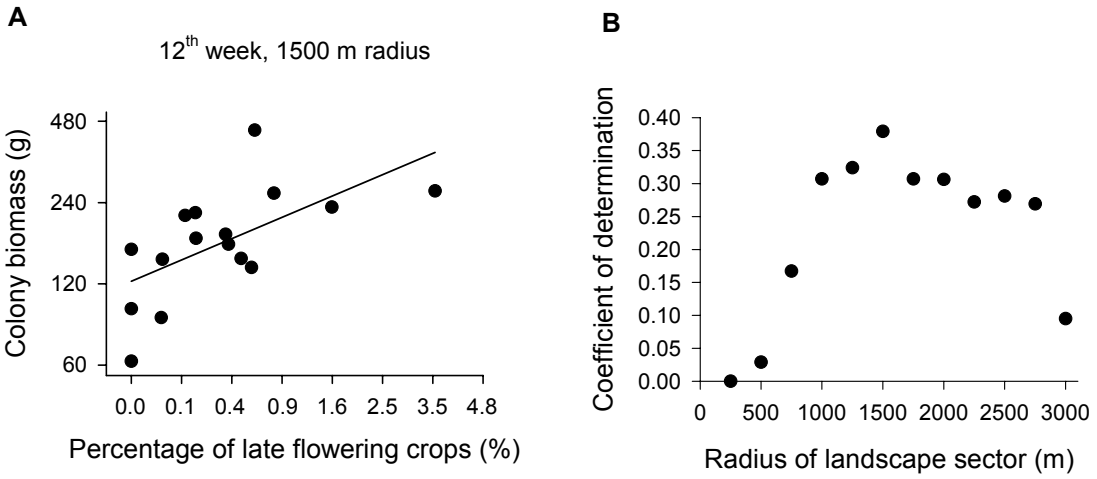

Fig. 6 Scale-dependent effects of the availability of late flowering crops on the colony biomass of *B. terrestris*. (A) Most explaining simple linear regression model: positive influence of the percentage of late flowering crops in landscape sectors with 1500 m radius on the colony biomass in the 12th week of the experiment ($F_{1,14} = 8.54$, $p = 0.011$, $r^2 = 0.379$). (B) Coefficients of determination for simple linear regressions between the percentage of late flowering crops and the colony biomass in the 12th week for 12 landscape sectors with 250 m – 3000 m radius. Regressions are statistically significant for landscape sectors with radii between 1000 m and 2750 m ($p < 0.050$, $n = 16$).

Discussion

Resource availability

For the successful completion of their colony cycle bumblebee colonies rely on an adequate provision with nectar and pollen throughout the season (Heinrich 1979, von Hagen 1994). Flowering crops and semi-natural habitats represent more or less rewarding resources in agricultural landscapes, which vary with their spatial and temporal availability (Fussell & Corbet 1991, Banaszak 1992, Corbet 1995).

Contrary to our expectation (Banaszak 1992, Corbet 1995), the amount of continuously available food plants (i.e. locally on the fallows or regionally in semi-natural habitats) did not affect the colony growth of *B. terrestris* at any spatial scale or any point in time.

However, the colony growth of *B. terrestris* was positively related to the availability of oilseed rape in the 5th and 8th week of the experiment. Likewise, we found a positive relationship between the availability of oilseed rape and bumblebee densities in a previous study (Westphal et al. 2003). Both findings indicate independently that bumblebee colonies benefit substantially from the availability of highly rewarding resources early in the colony cycle, i.e. at the time of colony founding and during production of the first worker generations.

In our landscape sectors oilseed rape was flowering until the 25 May 2002. As bumblebee colonies do not store great amounts of pollen and nectar (Heinrich 1979), the beneficial effects of highly rewarding mass flowering crops apparently translated directly into colony biomass. The plentiful provision of the brood and high brood temperatures, which could be attained owing to the constant nectar availability, led apparently to the development numerous and presumably large larvae or workers, respectively. The approximate three weeks development period of bumblebee brood (von Hagen 1994), might be the reason why the positive effects of available oilseed rape fields were detectable up to three weeks after the flowering of oilseed rape ceased.

Furthermore, the availability of late flowering crops had a positive effect on the biomass of the *B. terrestris* colonies in the 12th week of the experiment, indicating that highly

rewarding late flowering crops could possibly compensate the shortage of food plants, which often occurs in modern agricultural landscapes during the summer (Steffan-Dewenter & Kuhn 2003).

Although, according to the literature, most of the late flowering crops start to flower in June or July (Table 1) (Oberdorfer 1994), the significant effect of the availability of late flowering crops on the colony biomass occurred not until the 12th week of the experiment. At a certain point during the colony cycle bumblebees switch from the production of workers to the production of reproductives (Oster & Wilson 1978, Heinrich 1979). This "switching point" is presumably related to the numbers of workers in the nests, but also to the resource availability (Bowers 1985, 1986). Granted that most reproducing colonies have switched to the production of reproductives at some point during the flowering period of the late flowering crops, the colony biomass would achieve a maximum approximately two weeks later, when most larvae reach their last (and heaviest) stage (von Hagen 1994). Thus, by the 12th week of the experiment the differences between the biomass of successfully reproducing and already collapsing colonies were presumably fairly large. In the large and heavy colonies the first or even second clutch of reproductives could have developed owing to the copious supply with late flowering crops, whereas the small colonies were presumably dying of starvation, as sufficient resources were not available in the landscape.

It seems that the availability of forage is particularly crucial for bumblebee colonies at two sensitive points during their colony cycle: first, early in the season, when solitary queens are founding the colonies, and when later on the first workers take over the nest duties and foraging (von Hagen 1994). Second, in summer, when there are numerous workers in the nests, and the competition for resources might be high, as all colonies need sufficient food for their reproductive offspring (Bowers 1985, Pelletier & McNeil 2003). In this regard, highly rewarding resources appear to be particularly important for *B. terrestris*. But other bumblebee species should also benefit from the availability of copiously available food plants in agricultural landscapes (Westphal et al. submitted), especially when naturally occurring food plants are scarce.

Albeit semi-natural habitats provide continuously available food plants throughout the season (Banaszak 1992, Corbet 1995), the availability of semi-natural habitats in the

landscape sectors did not affect the colony growth. The amount of food plants on the fallows did likewise have no effect. These results are congruent with earlier studies that did not find any significant effect of the percentage of semi-natural habitats in agricultural landscapes on the densities of bumblebees (Steffan-Dewenter et al. 2002, Westphal et al. 2003).

Foraging range

The patterns of the plotted coefficients of determination indicate that *B. terrestris* workers perceived the resource environment at medium to large spatial scales, suggesting large foraging ranges (Fig. 5, Fig. 6) (Walther-Hellwig & Frankl 2000b, Chapman et al. 2003, Westphal et al. submitted). The bumblebees apparently exploited flowering crops in landscape sectors with radii between 1000 m and 3000 m.

Theoretical studies demonstrate that depending on resource quality and abundance, foraging flights over large distances could be energetically rewarding (Dukas & Edelstein-Keshet 1998, Cresswell et al. 2000). As the flower cover on the fallows was relatively sparse (i.e. on average less than 5 %), and *B. terrestris* usually prefers the exploitation of habitats with a copious supply of food plants (Sowig 1989, Walther-Hellwig & Frankl 2000b), foraging *B. terrestris* workers might have chosen to fly further and to exploit more rewarding resources (Heinrich 1975, Hill et al. 2001). This foraging decision could explain, why the local resource availability did not significantly influence the colony growth. However, other studies demonstrated that the local availability of food plants in subalpine meadows (Bowers 1986), and in suburban gardens (Goulson et al. 2002a) positively affected the colony growth. These contrasting results might be due to different resource environments: the flower rich subalpine meadows were surrounded by forests, which did not provide food plants (Bowers 1985), and the suburban gardens also provided a copious food supply (Goulson et al. 2002a), whereas in our experiment the fallows represented only a meager local resource.

Most interestingly, the patterns of the plotted coefficients of determination were basically the same for the scale-dependent effects of the availability of oilseed rape on two different parameters, i.e. on bumblebee densities (Westphal et al. 2003) and on the colony biomass of *B. terrestris* (Fig. 5), in two different years. In both studies the strongest effects occurred for landscape sectors with 3000 m radius. In addition, the effects of oilseed rape availability on the two parameters strengthened with increasing spatial scale.

Reproductive success

We found that large (i.e. heavy) *B. terrestris* colonies produced reproductives earlier (Fig. 3), and achieved greater reproductive success than small ones (Fig. 2). In addition, the biomass of the colonies was related to the resource availability in the landscape sectors (Fig. 5, Fig. 6). Hence, growth, survival and reproduction of bumblebee colonies seem to be limited by the food resources in agricultural landscapes (see also Bowers 1985, 1986). The low reproductive success of *B. terrestris* colonies (only 20 % of the colonies were successfully rearing both young queens and males) provided further evidence that in some agricultural landscapes the successful reproduction even of a common and highly adaptable bumblebee species, like *B. terrestris* (Williams 1982, von Hagen 1994), was resource-limited (see also Pelletier & McNeil 2003).

With respect to the question, whether the assumed optimal foraging behavior of bumblebees (Heinrich 1975, Pyke 1980) is directed to maximize some evolutionary meaningful currency (Bowers 1986), like the reproductive success, our experiment demonstrated indirectly that *B. terrestris* tended to exploit highly rewarding resources (if available), and therewith apparently maximized the overall colony reproductive fitness (by producing higher numbers of reproductives) (Pelletier & McNeil 2003). Our results strongly suggest that in agricultural landscapes the resource availability is a major factor affecting the reproductive success of bumblebee colonies.

However, there is considerable residual variation in our models, which might be due to several factors we could not account for: (a) predation and endo-parasitism (von Hagen 1994, Durrer & Schmid-Hempel 1995), (b) intrinsic factors of the colony, such as the queen's fecundity and queen-worker conflicts (Mehdiabadi et al. 2003), (c) competition (Steffan-Dewenter & Tscharntke 2000b, Steffan-Dewenter & Kuhn 2003), and (d) the microclimate on the fallows (Unwin & Corbet 1991).

Conclusions

Our results further the understanding of the relationship between resource availability and colony growth of bumblebees in agricultural landscapes, and provide a scientific basis for the development of future conservation measures for these important generalist pollinators. Divers and large bumblebee populations rely on the successful reproduction of the colonies. In agricultural landscapes mass flowering crops helped to assure the growth, survival and reproduction of *B. terrestris* colonies. In contrast, semi-natural habitats and naturally available food plants were possibly occurring in such low quantities that they could not recognizably influence the colony growth of *B. terrestris* in our landscape sectors. Nevertheless, semi-natural habitats represent the only continuously available food supply and essential nesting sites for bumblebees in agroecosystems (Banaszak 1992, Fussell & Corbet 1992b, Corbet 1995).

We conclude that future conservation schemes should enhance the resource availability in agricultural landscapes to promote bumblebee populations, and to sustain their vital pollination service. Effective conservation measures could be the establishment of various mass flowering crops that ideally flower throughout the season, but also the implementation of additional flower-rich semi-natural habitats (Banaszak 1992, Walther-Hellwig & Frankl 2000b). Furthermore, the floristic composition of existing semi-natural habitats should be improved (Fussell & Corbet 1992a, Corbet 1995). Owing to the large foraging ranges of bumblebees, these conservation measures can only be effective when they are implemented at a landscape scale (Chapman et al. 2003, Westphal et al. submitted).

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5 Resource availability affects the foraging trip duration of bumblebees

Abstract

The foraging behaviour of bumblebees has been shown to depend on characteristics of local resource patches, but effects of resource availability at a landscape scale are little known. The energetic costs for flights during foraging trips are negligible compared to the economic value of the long time spent on foraging trips. Thus, the duration of foraging trips might be an important factor determining the overall foraging success, colony growth and reproductive success of bumblebees. We analysed the duration of foraging trips and colony growth of *B. terrestris*, a common bumblebee in European agroecosystems, in contrasting resource environments.

We purchased six even-aged *B. terrestris* colonies of similar size. Three colonies were placed in rich resource environments (i.e. landscapes with mass flowering *Phacelia tanacetifolia* fields), and three colonies were placed in poor resource environments (i.e. landscapes with large amounts of scattered semi-natural habitats, which provided lower densities of food plants than *Phacelia* fields).

A total of 870 foraging trips of 220 marked *B. terrestris* foragers have been observed using automated camcorder recordings. The duration of foraging trips was significantly shorter in rich resource environments (65 ± 2.3 min) than in poor ones (82 ± 3.4 min). In addition, the colonies in rich resource environments (129 ± 40 g) gained significantly more weight than the colonies in poor resource environments (19 ± 7 g).

Availability of resources in the surrounding landscape affected the duration of foraging trips, and the colony growth of bumblebees. *B. terrestris* systematically exploited highly rewarding resources resulting in shorter foraging trips and higher foraging success, which translated into enhanced colony growth, and thus presumably higher reproductive success. We conclude that future conservation schemes should improve the spatial and temporal availability of pollen and nectar resources in agricultural landscapes to counteract the ongoing declines of bumblebees. The implementation of both mass flowering crops and semi-natural habitats with enhanced diversity and abundance of food plants could prove to be effective.

Keywords: Duration of foraging trips, *Bombus terrestris*, resource availability, colony growth, optimal foraging theory, patch choice, pollination, semi-natural habitats, mass flowering crops, camcorder recordings, *Phacelia tanacetifolia*.

Introduction

Survival, growth and reproduction of animals strongly depend on their ability to allocate food resources successfully. Optimal foraging theory predicts that foragers tent to maximise the long-term net rate of energetic gain ((gain - costs) / time) (reviewed in Krebs & Davies 1993, but see Schmid-Hempel 1987). Thus, foragers have to consider time and energy budgets while collecting food (e.g. Heinrich 1975, Pyke 1980).

For most animals food resources are patchily distributed in space and time (Hansson et al. 1995). To optimise the foraging success in a variable resource environment, animals should search and exploit systematically the most rewarding resources (Dreisig 1995). Consequently, they should relate the choice of a foraging patch to the density and spatial distribution of resources (e.g. to minimize travel time), as well as to resource quality (Pyke 1980, Cresswell et al. 2000, Hill et al. 2001). Optimal foraging theory predicts that the foragers should distribute themselves to available resources in a way that the individual net rate of energetic gain will be equalized (ideal free distribution) (reviewed in Krebs & Davies 1993). The spatial and temporal distribution of resources is particularly important for central place foragers, like bumblebees and other social insects, since numerous foragers of a colony concentrate in a single location (Hamilton & Watt 1970, Dukas & Edelstein-Keshet 1998).

Bumblebees (*Bombus* spp., Hymenoptera, Apidae) are vital pollinators in agroecosystems (Corbet et al. 1991, Williams 1996), where they rely on semi-natural habitats as important food resources (Banaszak 1992) and nesting sites (Fussell & Corbet 1992b, Kells & Goulson 2003). Semi-natural habitats provide diverse, but often scattered food plants, which are continuously flowering throughout the colony cycle from early spring to late summer (von Hagen 1994, Corbet 1995, Meek et al. 2002). Bumblebees also benefit from highly rewarding mass flowering crops, like *Phacelia tanacetifolia* (Williams & Christian 1991), which achieve higher flower densities than the food plants in semi-natural habitats, but bloom only over short periods of time (Westphal et al. 2003, Westphal et al. submitted). Intensification of farming practices considerably altered agricultural landscapes (Matson et al. 1997, Tilman et al. 2001). Diminishing amounts of semi-natural habitats, and changes in their floristic composition

might have caused the ongoing declines of bumblebee diversity and abundance in Europe and North America (reviewed in Goulson 2003).

In modern agricultural landscapes the survival, growth and reproduction of bumblebee colonies seems to be limited by the availability of resources (Goulson et al. 2002a, Pelletier & McNeil 2003, Westphal et al. submitted). As bumblebees presumably have large foraging ranges, they perceive their resource environment at large spatial scales (i.e. at landscape level) (Walther-Hellwig & Frankl 2000b, Westphal et al. submitted). The foraging behaviour of bumblebees has largely been investigated in single resource patches, or at local spatial scales (e.g. Hodges 1985, Dreisig 1995). To our knowledge, empirical studies comparing the foraging behaviour of bumblebees in different large-scale resource environments (e.g. at landscape level) have not been conducted yet. However, theoretical models indicate that bumblebees respond to different large-scale resource environments by adapting their foraging ranges and the duration of their foraging trips (Dukas & Edelstein-Keshet 1998, Cresswell et al. 2000).

During their foraging trips bumblebee foragers spend considerable amounts of time for (a) travelling between their nest and foraging patches, (b) searching rewarding patches, (c) flying between flowers within a patch, (d) handling of flowers, and finally (e) removing nectar and pollen from flowers (Pyke 1980). The economic costs of long lasting trips (i.e. the reduced amount of nectar and pollen that will be collected per unit time when foragers spend long time for travelling) restrict the overall foraging success of a bumblebee to a greater extent than the energetic costs of long foraging flights (Beutler 1951, Heinrich 1979).

The duration of foraging trips seems to be a crucial factor determining the foraging success of bumblebee colonies. We investigated possible differences between the duration of foraging trips and colony growth in contrasting large-scale resource environments, which differed in the spatial distribution and quality of food resources. Agricultural landscapes with mass flowering *Phacelia tanacetifolia* fields, and small amounts of semi-natural habitats were assumed to represent highly rewarding (i.e. rich) resource environments, because they provided clumped food plants with large amounts of nectar and pollen (Williams & Christian 1991). In contrast, agricultural landscapes with large amounts of semi-natural habitats were assumed to represent less rewarding

(i.e. poor) resource environments, as lower densities of food plants, and the scattered distribution of semi-natural habitats might cause longer, and more laborious foraging trips.

We recorded the duration of foraging trips and colony weights of *B. terrestris*, a common bumblebee species in European agroecosystems, in contrasting resource environments to test the following hypotheses: (a) the duration of foraging trips in rich resource environments is shorter than the duration of foraging trips in poor resource environments, and (b) *B. terrestris* colonies in rich resource environments gain more weight than *B. terrestris* colonies in poor resource environments, owing to shorter foraging trips, and thus presumably greater foraging success.

Materials and methods

Study region and study sites

The study was conducted in the rural countryside surrounding the city Göttingen in southern Lower Saxony, Germany. The study region 23 km east-west and 15 km north-south of Göttingen comprised agricultural land use types (arable fields and grasslands), forests, settlements, and various semi-natural habitats (orchard meadows, set aside fields, calcareous grasslands, woods, hedgerows, grassy banks and ditches).

Within the study region we selected six circular landscape sectors with 3000 m radius as study sites. Three landscape sectors represented highly rewarding (i.e. rich) resource environments, and three landscape sectors represented less rewarding (i.e. poor) resource environments. We chose the radius of 3000 m for the landscape sectors to cover the potential foraging range of *B. terrestris* (Walther-Hellwig & Frankl 2000b, Westphal et al. submitted). The experiment took place on a fallow in the centre of each landscape sector.

Table 1 Characteristics of the six landscape sectors (3000 m radius) representing rich and poor resource environments. Differences between landscape characteristics were analysed with t tests.

	Rich resource environment		Poor resource environment			
Parameter	Mean ± SE	Range	Mean ± SE	Range	t_4 value	p value
Semi-natural habitats (%)	4.7 ± 0.7	3.7 – 5.9	8.2 ± 0.5	7.6 – 9.2	-4.10	0.015
Distance to nearest *Phacelia* field (m) *	500 ± 26	450 – 540	2903 ± 97	2710 – 3001	-23.91	< 0.001

* In landscape sectors where no *Phacelia* occurred, we used 3001 m distance for statistics to account for the possibility that just outside our 3000 m radius a field might have been located.

The current land use in the landscape sectors was mapped in summer 2002 using land register maps with a scale of 1:5000. The land use maps were transferred into Geographical Information Systems (GIS, Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany) for landscape analysis. We calculated the percentage of semi-natural habitats, and the distance between the central fallow and the nearest *Phacelia tanacetifolia* field to characterise the different resource environments. The landscape sectors differed significantly in the amounts of semi-natural habitats, and in the availability of mass flowering *Phacelia* fields (Table 1). In the rich resource environments mass flowering *Phacelia* fields were available in the close surroundings of the central fallow (less than 600 m), whereas *Phacelia* fields were located only at large distances from the fallow (> 2700 m) in the poor resource environments.

Experimental design

We purchased six even aged *B. terrestris* colonies (approximately 30 workers and the founding queen) from STB Control, Aarbergen, Germany. On 3 August 2002 we placed one colony inside the nesting chamber of large wooden observation boxes on each central fallow. The observation boxes stood on top of four house bricks to prevent the intrusion of surface water. As *B. terrestris* usually nests below ground (Fussell & Corbet 1992b), the wooden boxes were equipped with a double roof covering for heat insulation to achieve a nest climate as close as possible to the natural conditions.

The bumblebees could leave or enter the nesting chamber via a valve, which could be opened or closed manually. The exit hole of the observation box was located at one side of a closed porch to prevent the direct incidence of light. The bumblebees reached the exit hole through a plexiglass tube (250 mm long, 20 mm diameter), which connected the nesting chamber with the porch. The nesting chamber and the porch were separated by the observation chamber for the mobile camcorder unit (see below).

During the experiment (from 3 August to 5 September 2002) we weighted the colonies every ten to twelve days to monitor the colony growth. The maximum weight gain of each colony was calculated as the difference between the maximum weight of the colonies and the colony weight at the beginning of the experiment.

We recorded the temperature in the observation boxes with HOBO Temperature Loggers (synoTECH Sensor und Messtechnik, Linnich, Germany) to control for potential temperature effects on the duration of foraging trips. The daytime temperatures were recorded in 90 min intervals between 5:45 and 21:15. Based on these data, the mean daytime temperature was calculated for each observational day and study site separately.

Recording of foraging trips

We recorded the duration of foraging trips of individual *B. terrestris* workers pairwise in two landscape sectors, one was representing a rich resource environment, and the other one a poor resource environment. One or two days prior to recording we marked the foraging workers of the respective colonies individually with small plastic number tags ("Opalithplättchen", Werner Seipp, Butzbach, Germany). In total 512 workers had been marked (316 workers in rich, and 196 workers in poor resource environments).

On the observational days we removed the plexiglass tube, and implemented a camcorder unit in the observation chamber of the wooden boxes. Within this unit the forages could move again through a plexiglass tube. When the foragers passed a reflection light scanner (Pepperl & Fuchs, Mannheim, Germany) underneath the plexiglass tube, a stroke magnet triggered the photo-shot function of the digital camcorder (Panasonic NV-DS27EG), so that in and out coming workers were recorded. On the recorded pictures the corresponding time of the day was shown. Based on this information we calculated the duration of individual foraging trips.

Between 7 August and 5 September 2002 four to six recordings were performed between 9:00 and 21:00 in each landscape sector. The differences in the number of recordings per landscape sector were due to accidental malfunction of the recording technique. In total we recorded 105 h in rich resource environments, and 122 h in poor resource environments.

For the statistical analysis we considered only foraging trips lasting between 10 min and 210 min. As short trips could be performed for orientation or defecation purpose (Capaldi et al. 2000, Spaethe & Weidenmüller 2002), we excluded them form our data set. We decided on an upper limit for the duration of foraging trips (210 min), to minimize possible artefacts in our data, which might be due to missing or blurred pictures of foragers: i.e. the calculated trip duration would double, if the camcorder recoding missed out a return and a consecutive departure of a forager. In the literature we found variable values for the maximum duration of foraging trips of *B. terrestris* (e.g. c. 150 min (Goulson et al. 2002b), 139 min (Spaethe & Weidenmüller 2002), 416 min (Osborne et al. 1999)). As the majority of the recorded foraging flights was shorter

than 210 min (96 %), we think a trip lasting 210 min represents an appropriate upper limit for our resource environments.

Statistical analysis

Data were analysed with SPSS 11.5 for Windows (SPSS GmbH Software, Munich, Germany). We used an analysis of covariance (ANCOVA, Type III sums of square) to examine possible differences between the duration of foraging trips in rich and poor resource environments, while controlling for effects of the mean daytime temperature (Krzanowski 1998). The individual bumblebees were treated as unit of replication, i.e. the variable "duration of foraging trips" represents the average time one individual spent foraging on a single observational day. Differences between landscape characteristics and the maximum weight gain of the colonies were analysed with t tests (Zar 1984). We used arcsine square-root transformation to achieve normality for the percentage data. If necessary, logarithmic transformation was applied to other variables to achieve normality (Zar 1984). Arithmetic means ± 1 SE for the non-transformed data are given in the text.

Results

Duration and number of foraging trips

Throughout 30 observations we recorded a total of 870 foraging trips of 220 bumblebees. We observed 54 % of the bumblebees merely on a single day. 29 % of the marked bees were recorded on two different days, and 13 % on three days. Only 4 % of the marked bees were observed on four to five days during the observational period. On average the foragers spent 71.74 ± 1.98 min on their daily trips (n = 385). 50 % of the recorded bumblebees performed more than one trip per day (on average 1.86 ± 0.06 trips per day, maximum eight trips per day, n = 385).

Resource environment and duration of foraging trips

The mean daytime temperature (20.6 ± 0.4 °C, minimum 16.2 °C, maximum 24.9 °C, $n = 32$) did not significantly account for variance in the ANCOVA model ($F_{1,382} = 0.243$, $p = 0.622$). For this reason we excluded the covariate from the model, and then performed a single factor analysis of variance (ANOVA), which revealed significant differences between the duration of foraging trips in rich and poor resource environments. As expected, the foraging trips of *B. terrestris* workers lasted longer in landscape sectors with large amounts of semi-natural habitats, which were assumed to provide scattered food resources (Fig. 1). The short duration of the foraging trips in the landscape sectors with *Phacelia* fields in the surroundings of the nests, indicate that the foragers exploited this highly rewarding resource systematically.

Colony growth

We found significant differences between the maximum weight gains of the colonies in the differentially rewarding resource environments: the colonies in the poor resource environments gained less weight than the colonies in rich resource environments (Fig. 2). Owing to shorter foraging trips to nearby *Phacelia* fields, the nests in the highly rewarding landscape sectors apparently increased their foraging rate, i.e. they collected greater amounts of nectar and pollen per unit time compared to the nests in landscape sectors, where no *Phacelia* fields were available, or located at large distance from the colonies.

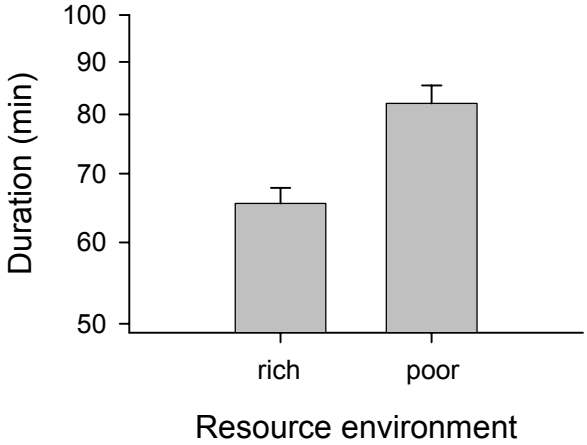

Fig. 1 Differences between the duration of foraging trips of *B. terrestris* workers in rich ($n = 239$, range 11 min - 181 min) and poor resource environments ($n = 146$, range 10 min - 209 min; ANOVA: $F_{1,383} = 17.23$, $p < 0.001$). The bars represent the mean + 1 SE.

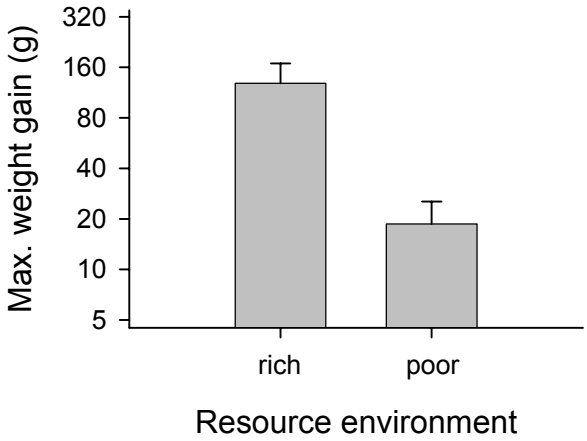

Fig. 2 Differences between the maximum weight gain of *B. terrestris* colonies in rich ($n = 3$), and poor resource environments ($n = 3$; t test: $t_4 = 4.168$, $p = 0.014$). The bars represent the mean + 1 SE.

Discussion

As mass flowering *Phacelia* fields represent more rewarding resources than semi-natural habitats (Williams & Christian 1991, Banaszak 1992, Corbet 1995, Williams 1997), we hypothesised that the foraging trips of *B. terrestris* workers would be shorter in agricultural landscapes where *Phacelia* fields were available, than in agricultural landscapes with large amounts of scattered, less rewarding semi-natural habitats. Owing to shorter search and travel times foragers should be able to gather the same amount of rewards (i.e. nectar and pollen) much faster in landscapes where they can exploit highly rewarding resources systematically (Heinrich 1976, Dreisig 1995). Consistent with our expectation, the duration of foraging trips was significantly shorter in rich resource environments than in poor ones (Fig. 1). The short duration of the foraging trips was due to the availability of nearby mass flowering *Phacelia* fields (Table 1), which apparently were systematically exploited by the foragers.

To our knowledge, this study provided first empirical evidence that the distribution of resources at landscape level affects the time bumblebees spend on their foraging trips. Consistent with our results, other studies in single resource environments indicated that foragers performed shorter foraging trips, or increased their foraging rates when resources were abundant (Allen et al. 1978, Thomson et al. 1987, Goulson et al. 2002b). Likewise, a theoretical model predicts that, if resources in nest vicinity were meagre, foragers should elongate the duration of their foraging trips to exploit more distant, and more rewarding foraging sites (Cresswell et al. 2000).

Once a bumblebee has discovered a rewarding foraging site, it will memorize the location, and exploit the site as long as it will be rewarding (site and flower constancy) (Heinrich 1976, Chittka et al. 1999, Osborne & Williams 2001). Thus, on future foraging trips it will have to spend less time searching for a rewarding site (Heinrich 1975). As semi-natural habitats usually provide more scattered and less abundant food plants than mass flowering *Phacelia* fields, foragers in *Phacelia* fields might have considerably reduced travel time between flowers (Waddington & Heinrich 1981). In addition, nectar and pollen in the open, shallow *Phacelia* flowers are easily accessible for the short-tongued *B. terrestris* workers (Williams & Christian 1991), so that

handling times would have been brief, too (Laverty & Plowright 1988). Provided that all *B. terrestris* foragers collected similar loads, the foragers in the rich resource environments could collect more rewards per unit time than the ones in the poor resource environments, which presumably had longer search, travel and handling times (Pyke 1980). The strong influence of *Phacelia* might be partly due to *B. terrestris*' preference for large foraging patches with rewarding, and easy to handle flowers (Sowig 1989, Walther-Hellwig & Frankl 2000b). Bumblebee species with other preferences might not benefit from *Phacelia* fields to the same extent, nevertheless their colonies also rely on rewarding foraging sites, and appropriate food plants, which should be available within their foraging ranges (Sowig 1989, Walther-Hellwig & Frankl 2000b, Westphal et al. submitted).

Regarding the overall foraging success of a bumblebee (i.e. net rate of energetic gain), the bumblebee's time and energy budget need to be considered (Pyke 1980, Cresswell et al. 2000). The time, which foragers spend flying between foraging sites and between flowers might constitute more then 80 % of a foraging trip (Heinrich 1979). In a case study (Heinrich 1979) demonstrated that the energetic costs for long distance flights are negligible compared to the economic costs of long lasting foraging trips: the nectar costs for a 24 min flight to a foraging site could be compensated by the exploitation of 24 additional flowers, which would only last 1 min. In contrast, a bumblebee, which is continuously foraging in nest vicinity, would collect more than triple the amount of nectar during the same time than the "long-distance forager" (provided that load size and floral rewards were similar). As the energetic costs of foraging are less constraining than the time an individual spends on foraging (Beutler 1951, Heinrich 1975), we assume that the foragers exploiting the *Phacelia* fields had a significant greater foraging success than the foragers, which had to rely on semi-natural habitats as food resources (Pyke 1980).

The colonies in rich resource environments gained significantly more weight than the colonies in poor resource environments (Fig. 2), indicating that the greater foraging success in landscape sectors with highly rewarding resources translated into improved colony growth, and therewith a better chance of successful reproduction (Bowers 1985, Goulson et al. 2002a, Pelletier & McNeil 2003, Westphal et al. submitted).

The individual foraging behaviour of bumblebees might be affected by the state and energy requirements of the colony (Cameron 1989, Cartar & Dill 1990, Cartar 1992). We minimised possible effects of the colony state on the duration of foraging trips by starting with equally sized and even aged colonies in our experiment. During the course of the experiment, the colonies developed differentially: the ones exploiting *Phacelia* fields established larger amounts of brood than the ones in the less rewarding resource environments. It has been demonstrated that foragers of honeybee colonies with large amounts of brood exhibited longer foraging trips than foragers of colonies with less brood (Eckert et al. 1994). Likewise, large amounts of brood in our colonies should have caused longer foraging trips. In contrast, we recorded significantly shorter foraging trips in the large colonies, suggesting that the foragers adjusted their behaviour to the contrasting resource environments, and not to the colonies' state. However, the foragers might also adapt their behaviour to other factors, such as risk sensitivity (Real 1981, Cartar & Dill 1990), or competition (Thomson et al. 1987).

In conclusion, bumblebees apparently modify their foraging behaviour in relation to large-scale resource availability. If highly rewarding resources are availably, *B. terrestris* foragers seem to exploit them systematically (Dreisig 1995). Although the less rewarding landscape sectors provided large amounts of semi-natural habitats, which are considered as important foraging habitats (Banaszak 1992, von Hagen 1994, Corbet 1995, Meek et al. 2002), *B. terrestris* benefited to a greater extent from the highly rewarding *Phacelia* fields. Owing to agricultural intensification, the diversity and abundance of food plants in semi-natural habitats has been substantially reduced (Fussell & Corbet 1991, Goulson 2003, Benton et al. 2003). Hence, we assume that the foragers found only limited amounts of rewarding food plants in the poor resource environments. Consequently, their foraging success was adversely affected by longer search and travel times (Pyke 1980, Cresswell et al. 2000).

Even in landscape sectors with large amounts of semi-natural habitats, the foraging success of *B. terrestris* was presumably limited by resource availability. For this reason, our results emphasise the need for future conservation schemes that consider the spatial and temporal availability, as well as the floristic composition of resource patches to sustain diverse and large bumblebee populations, and their vital pollination service in agroecosystems (Bronstein 1995, Williams 1996). Mass flowering crops can enhance

the population size of bumblebees, but should only represent additional resources, as they flower only over short periods of time, and do not offer suitable nesting sites (Fussell & Corbet 1992b, Walther-Hellwig & Frankl 2000b, Kells & Goulson 2003).

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Zusammenfassung

Als effiziente Bestäuber von Nutz- und Wildpflanzen übernehmen Hummeln (*Bombus* spp. (Latreille), Hymenoptera: Apidae) eine wichtige Funktion in Agrarökosystemen, die durch den fortschreitenden Rückgang ihrer Artenvielfalt und Häufigkeit beeinträchtigt werden könnte. Da Hummeln in der Agrarlandschaft vielfältige Ressourcen nutzen, die ihnen im gesamten Landschaftsgefüge zur Verfügung stehen, ist anzunehmen, daß ihre Populationsdynamik durch die räumliche und zeitliche Verfügbarkeit von Ressourcen auf der Landschaftsebene beeinflußt wird.

Über die Auswirkungen der Landschaftsstruktur auf die Populationsdynamik von Hummeln ist wenig bekannt. Deshalb standen Untersuchungen zum Einfluß der lokalen und regionalen Ressourcenverfügbarkeit auf die Dichten, das Koloniewachstum und die Sammelzeiten von Hummeln im Mittelpunkt der vorliegenden Arbeit. Zudem wurden indirekt die artspezifischen Sammelradien bestimmt.

Die Untersuchungen erfolgten in kreisförmigen Landschaftsausschnitten in der Umgebung von Göttingen, die sich hinsichtlich der Verfügbarkeit verschiedener Ressourcen, d.h. in den Flächenanteilen halbnatürlicher Lebensräume und Massentrachten, unterschieden. Die Ressourcenverfügbarkeit wurde für zwölf konzentrische Landschaftsausschnitte mit Radien zwischen 250 m und 3000 m (räumliche Skalenebenen) bestimmt und in Beziehung zu den ermittelten Kenngrößen gesetzt. Alle Experimente fanden auf je einer Brache im Zentrum der Landschaftsausschnitte statt.

Die Hummeldichten wurden in 16 experimentell angelegten *Phacelia tanacetifolia* Versuchsflächen erfaßt und in Beziehung zur Ressourcenverfügbarkeit in den unterschiedlich großen Landschaftsausschnitten gesetzt. Die Verfügbarkeit von halbnatürlichen Lebensräumen wirkte sich nicht signifikant auf die Hummeldichten aus. Zwischen den Flächenanteilen von Massentrachten (hauptsächlich Raps) und den Hummeldichten bestand ein signifikant positiver Zusammenhang, dessen Stärke mit der Größe der betrachteten Landschaftsausschnitte zunahm.

Um die artspezifischen Sammelradien zu bestimmen, wurden anschließend Zusammenhänge zwischen den Dichten einzelner Hummelarten und der Verfügbarkeit von Massentrachten auf den zwölf räumlichen Skalenebenen untersucht. Zwischen den Dichten der vier häufigen Hummelarten und der Verfügbarkeit von Massentrachten bestand jeweils ein positiver Zusammenhang. Die Dichten der großen Hummelarten *B. terrestris* agg. und *B. lapidarius* wurden von der Verfügbarkeit von Massentrachten in großen Landschaftsausschnitten am stärksten beeinflußt (3000 m bzw. 2750 m). Für die kleineren Arten *B. pascuorum* und *B. pratorum* wurden die stärksten Effekte auf mittleren bzw. kleinen räumlichen Skalenebenen festgestellt (1000 m bzw. 250 m). Scheinbar haben Hummeln artspezifische Sammelradien, die mit ihrer Körpergröße zusammenhängen.

Jeweils zwei *B. terrestris* Kolonien wurden auf 18 Brachen etabliert, um den Einfluß der lokalen und regionalen Verfügbarkeit von Nahrungsressourcen auf das Koloniewachstum zu analysieren. Weder die lokale noch die regionale Verfügbarkeit von Nahrungspflanzen in halbnatürlichen Lebensräumen beeinflußten das Koloniewachstum. Die Verfügbarkeit von früh- bzw. spätblühenden Massentrachten in großen Landschaftsausschnitten wirkte sich positiv auf das Koloniewachstum aus. Der Reproduktionserfolg der Kolonien hing von ihrer Größe ab. Die großen Kolonien brachten zu einem früheren Zeitpunkt eine größere Anzahl an Geschlechtstieren hervor als die kleinen Kolonien.

In Landschaftsausschnitten mit unterschiedlich ertragreichen Ressourcen wurden anhand von automatisierten Camcorderaufzeichnungen in sechs Kolonien 870 Sammelflüge von *B. terrestris* Arbeiterinnen erfaßt. In Landschaftsausschnitten mit besonders ertragreichen Ressourcen (*Phacelia* Felder) wurden signifikant kürzere Sammelflüge und zudem eine größere Gewichtszunahme der Kolonien festgestellt als in Landschaftsausschnitten mit weniger ertragreichen Ressourcen (halbnatürliche Lebensräume).

Aufgrund ihrer großen artspezifischen Sammelradien nutzen Hummeln in der Agrarlandschaft scheinbar Nahrungsressourcen auf der Landschaftsebene. Dabei hat sich insbesondere die Verfügbarkeit von Massentrachten positiv auf die Dichten, das Koloniewachstum und den Sammelerfolg von Hummeln ausgewirkt. Deshalb sollte die

Bedeutung der Massentrachten sowie die räumliche und zeitliche Verfügbarkeit von Nahrungsressourcen auf der Landschaftsebene bei der Planung zukünftiger Naturschutzmaßnahmen berücksichtigt werden. Aufgrund der oft kurzen Blühperioden von Massentrachten sind diese nur als zusätzliche, besonders ertragreiche Nahrungsressourcen geeignet. Folglich sollte auch die Verfügbarkeit und floristische Zusammensetzung halbnatürlicher Lebensräume in der Agrarlandschaft deutlich verbessert werden, um eine kontinuierliche Versorgung der Hummeln mit ausreichend Nektar und Pollen zu gewährleisten.

Summary

Bumblebees (*Bombus* spp. (Latreille), Hymenoptera: Apidae) pollinate a wide range of wild plants and crops in agroecosystems. This important ecosystem service might be endangered by the ongoing declines of bumblebee diversity and abundance. As bumblebees use various resources within the habitat pattern of agricultural landscapes, their population dynamics might be affected by the spatial and temporal distribution of resources at a landscape level.

However, little is known about possible effects of landscape structure on the population dynamics of bumblebees. Within the framework of this thesis, the influence of local and regional resource availability on the densities, the colony growth and the duration of foraging trips of bumblebees has been investigated. In addition, the species-specific foraging ranges have been identified.

The study was conducted in circular landscape sectors in the vicinity of Göttingen (Germany), which represented a gradient of resource availability, i.e. the landscape sectors differed in the amounts of semi-natural habitats and mass flowering crops. The availability of resources was quantified for twelve nested sub-sectors with radii between 250 m and 3000 m, which represented different spatial scales. All experiments were performed on a fallow in the centre of each landscape sector.

The densities of bumblebees were recorded in 16 experimental *Phacelia tanacetifolia* plots and related to resource availability at the different spatial scales. The availability of semi-natural habitats did not affect bumblebee densities at any spatial scale. However, bumblebee densities were positively related to the availability of mass flowering crops. The strength of the positive influence of mass flowering crops on bumblebee densities increased with spatial scale.

Based on this result, the densities of single bumblebee species were related to the availability of mass flowering crops at different spatial scales, to deduce the species-specific foraging ranges of bumblebees. The densities of four common bumblebee species were positively affected by the availability of mass flowering crops. The densities of the large bumblebee species *B. terrestris* agg. and *B. lapidarius* were most

strongly influenced at large spatial scales (3000 m and 2750 m, respectively). Whereas, for the smaller species, *B. pascuorum* and *B. pratorum*, the strongest effects occurred at medium and small spatial scales (1000 m and 250 m, respectively). Thus, foraging ranges of bumblebees seem to be species-specific and related to body size.

To investigate the effects of local and regional resource availability on colony growth, two *B. terrestris* colonies were established on 18 fallows. The local and regional availability of food plants in semi-natural habitats did not affect the colony growth. The availability of both, early and late flowering crops, had a positive influence on the colony growth at two different points in time during the colony cycle. The reproductive success of the colonies was related to their size, i.e. large colonies produced larger numbers of reproductives earlier in the colony cycle than small colonies.

Six *B. terrestris* colonies were placed in landscape sectors with differentially rewarding resources to investigate the duration of foraging trips and colony growth. A total of 870 foraging trips was videotaped by automated camcorders. In rich resource environments (i.e. landscape sectors with *Phacelia* fields) the duration of foraging trips was significantly shorter than in poor resource environments (i.e. landscape sectors with large amounts of semi-natural habitats). In addition, the colonies in rich resource environments gained significantly more weight than the colonies in poor resource environments, indicating a higher foraging success.

Owing to their large, species-specific foraging ranges, bumblebees are able to exploit resources in agricultural landscapes at a landscape level. The availability of mass flowering crops positively influenced the densities, the colony growth and the foraging success of bumblebees, particularly at a landscape level. Hence, future conservation schemes should consider the importance of mass flowering crops, as well as the spatial and temporal availability of resources at a landscape level. Mass flowering crops usually bloom for short periods of time, thus, they should represent supplementary, highly rewarding resources in agricultural landscapes. In addition, the availability and floristic composition of semi-natural habitats should be improved to provide a continuous supply of sufficient amounts of nectar and pollen for the bumblebees in agricultural landscapes.

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