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„Production- and population-ecological analysis of the
Mediterranean harvester ant *Messor wasmanni*
(Hymenoptera: Formicidae) “

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This thesis is dedicated to my family.

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Publications arising from this thesis

Production- and population-ecological analysis of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae)

Tanja Traxler

This thesis is based on the following manuscripts, which are referred to in the text by their Roman numerals.

Paper I: Traxler T. (2016) Native food spectrum, size-matching and foraging efficiency of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae). *Ecologica Montenegrina*, 7: 451-463.

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Paper II: Traxler T. (2016) The impact of predation by the myrmecophagous spider *Zodarion elegans* (Araneae: Zodariidae) on the activity pattern of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae). *Ecologica Montenegrina*, 7: 328-344.

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1. Zusammenfassung

Ameisen, welche Pflanzensamen sammeln und diese in Kammern ihrer Nester lagern beeindruckten schon seit jeher Menschen die von selbiger Aktivität in Wüsten oder im mediterranen Raum leben. Angefangen vom Buch des Salomons bis zu den alten Schriften der Griechen und Römer, haben sich Ernteameisen schon sehr bald in der westlichen Kultur als Symbol von Fleiß und Sorgfalt etabliert. Dieses metaphorische Bild wurde vor allem durch Ernteameisen der Alten Welt, welche der Gattung *Messor* Forel, 1890 angehören, geprägt (Hölldobler & Wilson 1990). *Messor wasmanni* Krausse, 1910 Ernteameisen, von welchen die vorliegende Dissertation handelt, besiedeln ausschließlich mediterrane Gebiete Südeuropas (Bračko *et al.* 2014).

Freilanduntersuchungen wurden auf der kroatischen Insel Cres, SSW zur Halbinsel Istriens durchgeführt. *M. wasmanni* Ernteameisen kommen auf Cres ausschließlich in der mediterranen Vegetationszone bzw. im mediterranen Klima vor.

Im Fokus der Freilanduntersuchungen für den ersten Teil (**Publikation I**) der Doktorarbeit stand u.a. die Erfassung des nativen Nahrungsspektrums der mediterranen Ernteameise *M. wasmanni*, sowie die Quantifizierung der ins Nest eingebrachten Materialien über eine Vegetationsperiode hinweg. Ferner wurde die „harvesting efficiency“ (der Anteil der mit Nahrung in das Nest zurückkehrenden Arbeiterinnen per Größenklasse von der Gesamtanzahl der zurückkehrenden Arbeiterinnen per Größenklasse) untersucht, und die Frage geklärt, ob auch bei dieser Ernteameisenart ein Verhältnis zwischen der Körpergröße der Ameise und der Größe der getragenen Ladung („size-matching“) besteht.

Ergebnisse zeigen, die granivore Ernährungsweise charakteristisch ist für die einzelnen Ameisenarten der Gattung *Messor*, *M. wasmanni* inbegriffen (Hahn & Maschwitz 1985, Hobbs 1985, Reyes-López & Fernández-Haeger 2002). Dies bedeutet, dass ein Großteil des Nahrungsbedarfs durch Pflanzensamen gedeckt wird. Dennoch werden gelegentlich auch tierische Überreste, unter anderem diverse Arthropoden sowie tote Schnecken, aber auch maritime Schnecken einsammelt.

Nahrung wird entweder in einzelnen kleineren Arealen gesammelt, oder in größeren, zusammenhängenden Gebieten. Entsprechend den gegebenen Bedingungen passen Arbeiterinnen ihre Strategien der Nahrungssuche („foraging strategies“) an. Bei geringem Nahrungsvorkommen suchen Arbeiterinnen alleine nach Nahrung („individual foraging“). Bei reichhaltigen und beständigen Nahrungsvorkommen werden Ameisenstraßen gebildet, auf denen Arbeiterinnen in großer Anzahl Nahrung zum Nest transportieren („column foraging“). *M. wasmanni* Kolonien formen Ameisenstraßen, welche eine Länge von bis zu 27.6 m erreichen können. Diese Ameisenstraßen werden frei von Vegetation gehalten. Sie entspringen am äußeren Rand der Nestoberfläche als breite Bahn, welche sich in einzelne Äste und schließlich in kleine Zweige aufteilt. Diese terminalen Zweige können sich täglich in Abhängigkeit des Nahrungsvorkommens verschieben.

Ergebnisse zeigen, dass *M. wasmanni* Arbeiterinnen beim Eintragen der Nahrung kein „size-matching“ anwenden. Das bedeutet, dass die Größenvariation der getragenen Ladung wenig bis nicht im Zusammenhang mit der Körpergröße der Arbeiterinnen steht. Ein weiteres Ergebnis

dieser Studie weist darauf hin, dass auf stark frequentierten Ameisenstraßen nicht nur größere Mengen an Nahrung ins Nest befördert werden, gleichzeitig steigt als Funktion der Kolonie-Aktivität, die Proportion an beladenen Arbeiterinnen an der Gesamtanzahl der ins Nest zurückkehrenden Arbeiterinnen per Größenklasse. Zusätzlich variiert die „harvesting efficiency“ in Abhängigkeit von der Körpergröße der Arbeiterin von Mai bis Oktober 2009. Dieses Ergebnis weist darauf hin, dass der individuelle Metabolismus der Arbeiterinnen eine wichtige Rolle bei der „harvesting efficiency“ spielt.

Im Focus der Freilandarbeiten für **Manuskript I** steht zum einen die Beschreibung der Nestoberflächen von *M. wasmanni* Ernteameisenkolonien, zum anderen das Einsammeln des auf den Nestoberflächen angehäuften Abfallmaterials „chaff pile“ aus dem Norden (Merag, Loznati), der Mitte (Zaglav, Belej) und dem Süden (Osor, Punta Križa) des Verbreitungsgebietes von *M. wasmanni* Kolonien auf der kroatischen Insel Cres. Im Labor wurde dieses Abfallmaterial sowohl einer qualitativen als auch quantitativen Analyse unterzogen.

Bei allen untersuchten Nestern befand sich das Abfallmaterial am äußeren Rand der Nestoberfläche. Auch die Analyse des Abfallmaterials weist darauf hin, dass sich *M. wasmanni* Ernteameisen vor allem von Pflanzensamen ernähren (Granivorie), aber dennoch konsumieren sie gelegentlich auch Insekten und Schnecken. Pflanzliches Material macht einen Anteil von 90.9% aus und umfasst 55 Pflanzenarten aus 20 Familien. 21 Typen pflanzlicher Diasporen und andere Pflanzenteile wurden identifiziert. Samen sind mit einer relativen Häufigkeit von 7.5% im Auswurfmaterial vertreten. Der relativ hohe Anteil an noch intakten Samen im Abfallmaterial weist darauf hin, dass einzelne Kolonien, obgleich ihrer granivoren Ernährungsweise, eine bedeutende Funktion in der Weiterverbreitung von Samen einnehmen. Ernteameisen können durch Verlust von Samen beim Transport, vergessene Lagerstätten im Nest oder der unbeabsichtigten Entsorgung von noch intakten Samen zur Verbreitung von Pflanzensamen beitragen.

Der restliche Anteil von 9.1% setzt sich aus tierischen Überresten und Faeces zusammen. Insgesamt wurden 43 tierische Taxa identifiziert. Es wird angenommen, dass der gelegentliche Verzehr von Insekten und Schnecken eine zusätzliche Proteinquelle darstellt (Azcarate *et al.* 2005), vor allem, wenn pflanzliche Nahrung im Frühjahr noch rar ist oder, wenn pflanzliche Nahrung während länger andauernden Dürreperioden stark reduziert ist.

Forschungsziel der Freilanduntersuchungen für **Publikation II** der Dissertation war die Analyse des täglichen Aktivitätsrhythmus der mediterranen Ernteameise *M. wasmanni*. Beobachtungen im Zuge der Felduntersuchungen weisen darauf hin, dass nicht nur mikroklimatische Faktoren (Ruano *et al.* 2000, Azcarate *et al.* 2007, Cole *et al.* 2010), sondern auch biologische Faktoren wie Prädation Einfluss auf den Aktivitätsrhythmus einzelner *M. wasmanni* Kolonien zu nehmen schienen. Wiederholt wurde das Vorkommen von Spinnen, welche sich auf die Jagd von *M. wasmanni* Arbeiterinnen spezialisiert hatten, beobachtet. Hierbei handelt es sich meist um die obligat myrmecophage Spinne *Zodarium elegans* (Simon, 1873). Aus diesem Grund wurde der Schwerpunkt der Freilanduntersuchung auf die Reaktion von *M. wasmanni* Ameisenkolonien auf Prädation durch *Z. elegans* gelegt. Diesbezüglich wurden auch Laborexperimente durchgeführt, in denen untersucht wurde, wie sich Prädation durch *Z. elegans* auf den Aktivitätsrhythmus einer *M. wasmanni* Ameisenkolonie außerhalb des Nestes auswirkt. Zusätzlich wurde die Dynamik zwischen Aktivitäten außerhalb des Nestes und Aktivitäten innerhalb des Nestes unter Anwesenheit von Prädatoren analysiert und untersucht wie sich Prädation auf die Arbeitsteilung

in Bezug auf Körpergröße der Arbeiterinnen innerhalb des Nestes auswirkt. Zu diesem Zweck wurde eine *M. wasmanni* Kolonie bei Martinšćica (Cres, Croatia) ausgegraben und in ein Formicarium im Labor eingesiedelt. *Z. elegans* Individuen wurden ebenfalls gefangen und ins Labor transferiert.

Ergebnisse demonstrieren, dass Ameisenkolonien als Reaktion auf Prädation ihre Aktivitäten außerhalb des Nestes temporär stoppen und die Nesteingänge verschließen. Der Nestverschluss hat einerseits den Nutzen, dass obligat myrmecophage Spinnen wie *Z. elegans* nicht ins Nest eindringen können, andererseits, dass Prädatoren unter natürlichen Bedingungen inaktive Ameisenkolonien verlassen und zu aktiven Kolonien in unmittelbarer Nähe wechseln.

Unter Laborbedingung ist die Erbeutung einer einzigen Arbeiterin ausreichend, um den Verschluss der Eingänge am Ende der Aktivität außerhalb des Nestes auszulösen. Die Nesteingänge bleiben bis zu sechs Tage geschlossen. Ferner konnte Polyethismus in Hinblick auf morphologische Größenunterschiede in der Arbeiterklasse festgestellt werden. Kleine Arbeiterinnen (Minor-Arbeiterinnen) sind ausschließlich am Verschluss der Nesteingänge beteiligt, wohingegen größere Arbeiterinnen (Medium-, und Major-Arbeiterinnen) zusätzlich zum Nestverschluss Prädatoren wie myrmecophage Spinnen der Spezies *Z. elegans* attackieren und verjagen.

Flexibilität in der Ausführung einzelner Aufgaben ist essentiell für ein robustes System der Arbeitsteilung in einer *M. wasmanni* Kolonie. Ergebnisse zeigen, dass Störungen die ausschließlich Aktivitäten außerhalb des Nestes betreffen, ebenfalls auf die Intensität der Ausführung einzelner Aktivitäten im Inneren des Nestes Einfluss nehmen. Darüber hinaus werden die Nesteingänge verschlossen und jene 24% der Arbeiterinnen der Laborkolonie, welche im Normalfall vor allem Aktivitäten außerhalb des Nestes durchführen, müssen ebenfalls im Inneren des Nestes verbleiben. Nur ein kleiner Anteil der farblich markierten Arbeiterinnen beteiligt sich bei geschlossenen Nesteingängen an der Nahrungsweiterverarbeitung. Die große Mehrheit bleibt jedoch inaktiv oder putzt sich.

Diese Arbeit gibt neue Einblicke in das Nahrungsspektrum, sowie in die Auswirkungen von Prädation durch die myrmecophage Spinne *Z. elegans* auf die Aktivität von *M. wasmanni* Ernteameisenkolonien.

2. Abstract

Harvesting of seeds by ants in deserts and grassland impresses human beings who live by the same activity since a long time. Additionally, the storing of seeds by ants in underground granaries of their nests has equal appeal. Starting, from the Book of Solomon to the texts of the ancient Greeks and Romans, ants were established very early in the Western culture as the symbols of productiveness and prudence. The metaphorical view of these insects was mainly shaped by abundant Old World harvester ants of the myrmicine genus *Messor* Forel, 1890. The generic name comes from the Roman god of crops and harvest, Messor (Makhan *et al.* 2011).

This doctoral thesis is about the Mediterranean harvester ant *Messor wasmanni* Krausse, 1910, a common seed predator in the Mediterranean grasslands with the distribution from Italy to the Balkan Peninsula and Turkey (Bračko *et al.* 2014). The study area was located on the Croatian island of Cres, SSW to the peninsula of Istria. *M. wasmanni* harvester ants only occur in areas of Mediterranean climate on the island Cres.

In the first part of the doctoral thesis (**Paper I**), it was assumed that *M. wasmanni* ant colonies are able to maximize the acquisition of food resources by both (a) fitting the spatial distribution of foragers with the distribution of food items and (b) adapting foraging behavior to environmental conditions. Accordingly, the main objectives of the present study were to analyze: 1) the native food spectrum of *M. wasmanni* harvester ants and 2) aspects of foraging comprising size-matching (the relation between ant size [mm] and load size [mm]) as well as harvesting efficiency (the proportion of returning laden workers per size class of the whole number of returning workers per size class to the nest) under natural conditions.

Results show, that *M. wasmanni* workers form narrow and cleared trunk trails, reaching a total length of up to 26.7 m. These trunk trails are typically dendritic in their form and are used for foraging. Each trail arises as a single broad pathway on the outer rim of the nest surface, then diverges into branches and finally into twigs. These terminal twigs shift from day to day, whereas trunks and branches persist over months. Food items were gathered either from several distinct small regions by individual foraging or from zones with rich food availability by column foraging. Accordingly, the foraging strategies are a mixture of individual foraging and column foraging, adjusted to the workers' needs (Hölldobler & Wilson 1990, Traxler 2016a). Moreover, under natural conditions, *M. wasmanni* workers do not show size-matching at foraging trails. Little, if any, size variation of collected loads can be attributed to the forager's body size.

This study showed that, on highly frequented, cleared foraging trails, *M. wasmanni* foragers brought not only greater quantities of food items to the nest, but also the proportion of laden ants over the total number of incoming foragers per size class increased as a function of colony activity. Moreover, harvesting efficiency varied between worker size classes (minor-, media- and major-workers) from May to October 2009. This finding suggests that the worker size and the resulting difference in individual metabolism play an important role for the harvesting efficiency of *M. wasmanni* workers.

Under natural conditions, the diet of *M. wasmanni* is composed almost entirely of seeds from a wide spectrum of plant species (granivory). Granivory is a feature common to numerous species of the *Messor* Forel, 1890 genus (Hahn & Maschwitz 1985, Hobbs 1985, Reyes-López &

Fernández-Haeger 2002). Yet, *M. wasmanni* workers occasionally gathered animal remains comprising a variety of arthropod fragments, dead land snails, as well as dead marine gastropods.

In the second part of the doctoral thesis (**Manuscript I**) fieldwork was conducted to analyze the nest surface of the Mediterranean harvester ant *M. wasmanni*. Furthermore, chaff pile material of *M. wasmanni* colonies was collected from the northern (Merag, Loznati), the middle (Zaglav, Belej) and the southern region (Osor, Punta Križa) of the distribution area on the Croatian island of Cres. In the laboratory, a detailed qualitative and quantitative analysis of plant species and plant parts present in chaff piles was made on each sample separately.

Chaff piles generally are located at the outer edge of nest surfaces. Plant material accounts for 90.9% of the total quantity of the chaff pile material and comprised 55 plant species of 20 families. This broad spectrum of food plants can be reinforced by the fact that in physically demanding and irregular environments in which harvester ants occur, only few plant species produce a profitable crop of seeds during any given year. Furthermore, chaff pile material comprised a total of 21 types of dispersal units and other plant parts. Seeds occurred with a relative frequency of 7.5% in chaff piles. *M. wasmanni* harvester ants feed on the seeds themselves (granivory). Yet results show that their effect on the plants they visit is not wholly negative. They also disperse plants because from time to time they lose seeds along their foraging trails or they discard seeds by accident on the chaff piles. In this way, they compensate in part the damage caused by seed predation (Hölldobler & Wilson 1990).

Results show, that although, chaff piles of *M. wasmanni* colonies are primarily composed of seeds and other diaspores from a wide spectrum of plant species, they comprise to a minimum extent animal remains (arthropod corpses, orthoptera-faeces or snails) as well. Animal remains and faeces represented a share of 9.1% of the chaff pile material. A total of 43 animal taxa were identified. Results underline that animal remains probably represent a complementary protein source (Azcárate *et al.* 2005) in the diet of *M. wasmanni* harvester ants, especially when seeds and fruits are scarce in spring and during periods of drought.

Previous observations during field studies suggest that the activity pattern of *M. wasmanni* colonies is not only modified by microclimatic conditions (Ruano *et al.* 2000, Azcárate *et al.* 2007, Cole *et al.* 2010), but also by biological factors, such as predation. Numerous *Zodariion elegans* (Simon, 1873) spiders were observed preying on *M. wasmanni* workers during aboveground activity. Consequential, the central objective was to determine the effect of predation by the zodariid, obligate myrmecophagous spider *Z. elegans* (these spiders depend solely on ants as a food source), on the activity pattern and behavior of the Mediterranean harvester ant *M. wasmanni* (**Paper II**). For laboratory research, a *M. wasmanni* colony and mature *Z. elegans* individuals were transferred to the laboratory.

In this study, it could be shown that *M. wasmanni* colonies respond in two different ways to spider predation. They 1) attack the invader, and 2) they temporarily stop all foraging activities outside the nest and close nest entrances. Consequently, obligate myrmecophagous spiders such as *Z. elegans*, usually leave inactive colonies and move to active ones nearby (Traxler 2016b). Moreover, observations under laboratory conditions show that the capture of a single ant is sufficient to trigger cessation of foraging activities and closure of nest entrances with 100% confidence. Furthermore, polyethism occurs by means of morphological differences (size classes) among *M. wasmanni* workers. Minor workers were only engaged in nest closure; while larger

works (media and major workers) additionally attacked, and drove *Z. elegans* spiders away from the colony (Traxler 2016b).

Finally, a study on the dynamics of task allocation by asking how the tasks are related was started. The question was whether perturbation outside the nest such as predation by the myrmecophagous spider *Z. elegans* would affect the intensity of activity performance of the inside workforce. Results show that events that directly affect workers engaged in one task outside the nest also cause changes in the intensity of task performance inside the nest. The capture of a single ant is sufficient to trigger cessation of exterior activities and the closure of nest entrances. Resulting, all exterior workers stay inside the nest when entrances are closed. It was analyzed, if exterior workers also perform interior activities as a result of nest closure. Behavioral observations were made on marked foragers to determine how flexible they are in response to predation pressure. Only a small proportion of marked foragers switched to food processing while the majority was inactive or grooming during inactivity outside the nest.

This thesis gives new insights in the food spectrum, and the effect of predation by the myrmecophagous spider *Z. elegans* on the activity of *M. wasmanni* harvester ant colonies.

3. General Introduction

Harvester ant is a general designation for any of the species or genera of ants that collect seeds (seed predation or granivory), which are then stored in the nest in communal chambers called granaries. Harvester ants occur in various subfamilies (Ponerinae, Myrmicinae, und Formicinae) and genera: *Messor* Forel, 1890 (more than 100 species), *Pheidole* Westwood, 1839 (more than 1000 species) and *Pogonomyrmex* Mayr, 1868 (about 60 species). The *Veromessor* Forel, 1917 genus was recently added to *Messor*, adding 8 more species (Hölldobler & Wilson 1990). Harvester ants are distinguished from the group of ant species that collect elaiosomes, which are nutritive appendages on the seeds (Hölldobler & Wilson 1990). Foragers discard seeds on the way to the nest as soon as they have detached the elaiosomes. They are therefore major seed dispersers of myrmecochorous plants. In contrast, harvester ants feed on seeds themselves. Yet, their impact on the plants is not entirely negative because from time to time they accidentally abandon viable seeds along foraging trails or discard them by accident at the nest surface. Resulting, they compensate at least in part the damage caused by seed predation (Hölldobler & Wilson 1990).

3.1. Distribution

Harvester ants are dominant elements in deserts, Mediterranean habitats and in warm temperate, as well as tropical regions around the world, particularly in North America, Australia, the Sahara, and South Africa (Wehner 1987). Most of the *Messor* ant species originated in dry regions of the Northern Hemisphere. *M. wasmanni* is a Mediterranean harvester ant occurring from Italy and Corsica to the Balkan Peninsula and Turkey (Bračko *et al.* 2014).

3.2. The colony structure

An ant colony comprises almost entirely of females. Males remain in the nest only until the time of their nuptial flight and they die after mating (Hölldobler & Wilson 1990). Consequently, the queen must raise her young colony alone. Because male ants develop from unfertilized eggs they only have half the number of chromosomes than their sisters and mothers.

The first level of colony construction is sociogenesis, the growth of a colony by the development of castes that act together as a functional whole. Hölldobler & Wilson (2009) asserted that castes are created by algorithms of development, the sequential decision rules, that guide the body growth of ants step by step until the insect reaches its adult stage. In social insects, such as ants, bees and wasps, the sequence is roughly as follows. At the first decision point, depending on its physiological condition, the developing female egg or larva is pushed onto the one or the other of two paths of development. If the immature insect should take the path leading to more extended growth and development, it will turn into a queen upon reaching the adult stage. In contrast, if it takes the second path, it will curtail growth and development and end up as worker. Additionally, in several ant species, the worker-bound larva encounters a second decision point on the way to adulthood. One path leads the larva to maturity as a major worker called “soldier”, while the other path leads it to maturity as a minor worker (Hölldobler & Wilson 2009).

Workers acting together as functional unit that are guided by sets of behavioral rules, operating in the following manner. If in a given context the worker encounters a certain stimulus from the environment, it predictably performs a certain type of behavior, and if the same stimulus is received in a different context, the worker will perform a different act. If the worker detects for instance a hungry larva in the brood chamber, the worker will offer it food. But if the worker finds the larva elsewhere in the nest, the worker will carry it, whether hungry or not, to the brood chamber (Hölldobler & Wilson 2009).

A single worker has a repertoire of a few dozen acts. The totality of these relatively sparse and simple responses defines the behavior of a colony. A colony of social insects is characterized by self-organization. Instead, there is no overseer who carries a master plan in the head. The superorganism exists in the separate programmed responses of the individuals that compose it (Hölldobler & Wilson 2009).

Which of the insect societies deserve to be designated as superorganism? In the broader sense, the term superorganism is appropriate for eusocial insect colonies, in which three traits are combined: first, adult colony members are divided into a reproductive caste and into a partially or wholly nonreproductive caste. Second, individuals of at least two generations coexist in a colony; and third, nonreproductive or less reproductive workers care for the young. In a superorganism, the interindividual conflict for the reproduction privilege is diminished and workers are selected to maximize the colony efficiency (Reeve & Hölldobler 2007).

3.3. Principles of the evolution of castes

Hölldobler & Wilson (2009) listed three trends in the evolution of labor in ants. First, in a few of the anatomically and socially most primitive ant species and in early stages in colony growth of several other ant species as well, the division of nonreproductive labor among workers is very weak or absent. The labor in this lower evolutionary grade is divided according to current needs as perceived by individual workers. Unoccupied workers patrol inside as well as outside the nest while foraging for work, or they are recruited by nestmates to sites short on labor.

Second, in ant species that have evolved more complex societies, true castes appear. Individual workers devote long periods of their lives to certain tasks, such as brood care, construction of the nest or foraging for food outside the nest. In most of these ant species, castes are primarily physiological, displaying at most weak differences among workers in size and anatomy. These caste systems are the results either of dominance relations among workers, age of workers or differences in experience of workers.

Third, the trend toward larger and more complex ant societies has been accompanied by a strengthening of mechanisms that differentiate worker subcastes and labor roles. The most extreme of such diversification is achieved in the minority of ant species that express physical castes. Within the physical castes there are folded more finely differentiated physiological castes. Such theoretically perfect labor system consists of a specialist for each type of labor. Each labor role would be performed in proportions appropriate to the colony's needs. In reality, ant castes fall far short of that level (Wilson 1968). The diversity of castes is strongly constrained by moment-to-moment decisions, unpredictable environmental shifts and the exigencies they impose on the ant colony. Workers are forced to be able to change from one labor role to another, often within a few minutes in order to achieve maximum colony efficiency (Hölldobler & Wilson 2009).

3.4. Activity pattern

In literature the most common activity pattern of foraging in hot and dry climates is described as bimodal, in which the activity is peaking in the cool of the morning and then again as the temperature is decreasing in the afternoon or early evening. Yet, this feature is evidently very dependent on microclimatic conditions such as temperature and humidity (Hölldobler & Wilson 1990). With the onset of the cooler season this pattern changes from bimodal to unimodal, where the peak shifts to midday or early afternoon. At the beginning of a daily foraging period, foragers emerge very quickly in columns that follow along existing trunk trails (Hölldobler & Wilson 1990).

3.5. Granivory

Granivory terms the interaction between plants and seed-predators that feed largely or completely on seeds. Seeds can be described as products of the fertilized ovules of flowering plants. They consist of an embryo, of food-storage organs and of a protective seed coat called testa (Leins & Erbar 2008). Many animal species including harvester ants feed on seeds (Hahn & Maschwitz 1985, Hobbs 1985, Reyes-López & Fernández-Haeger 2002). Frequently, a distinction is made between pre-dispersal seed-predators that feed on seeds on the parent plant before they are dispersed and post-dispersal seed-predators that forage for seeds after they have been dispersed. However, many granivores act as both pre- and post-dispersal predators (Herrera & Pellmyr 2009).

Harvester ants collect food items, such as seeds, other diaspores and plant parts, and store them in specific granaries within their nest. Within these granaries, seed germination and disintegration by mushrooms and bacteria are prevented by the use of a metapleural glandular secretion (Schildknecht & Koob 1971, Celli & Maccagnani 1994). With this treatment food items are preserved for periods of inactivity outside the nest, so that low seed production in spring (Kirchner 2001), as well as inactivity outside the nest as a result of predation (MacKay 1982) can be overcome easily.

3.5.1. Foraging strategies

The success of harvester ants is not due entirely to their heavy reliance on stored seeds, but additionally to three traits that impart flexibility in foraging strategies:

Individual and column foraging

First, the foraging strategy of harvester ants of the genus *Pogonomyrmex* and *Messor* is a mixture of both individual and column foraging, adjusted to the needs from day to day. Patrollers go forth to explore the surrounding area. They are directed by: 1) visual landmarks, 2) their compass direction relative to the sun and 3) odor marks deposited in the vicinity of the nest exits (Hölldobler 1971b). If a worker discovers a solitary seed, it will be carried back to the nest. But if a worker discovers a patch of seeds, she carries one seed back to the nest and simultaneously she deposits an odor trail from the tip of her abdomen. Resulting, further nestmates travel out to the

seed patch along the trail, and while returning to the nest with burdens they add trail pheromones as well. In time, if the seedfall persists over a longer period of time, the chemical deposits accumulate in sufficient strength to establish a trunk trail, along which great numbers of workers travel back and forth. In this way, ant colonies shift more from individual foraging to foraging along trunk trails (column foraging). Even in times of rich food offer, a few patrollers wander away from the main routes. Resulting, they occasionally discover new sources of food. Individual and column foraging together provide the harvester ant colony with the flexibility of response needed to exploit the entire surrounding environment efficiently. By this process the outer reaches of the trunk-trail system shift subtly from day to day (Hölldobler & Wilson 1990).

Trunk trails

Second, harvester ant colonies rotate their trunk trails around their nest in a way that brings them repeatedly to new seed patches. In this way, harvester ant colonies increase their yield over long stretches of time.

Numerous species in the Myrmicinae, Dolichoderinae, and Formicinae lay trunk trails that are traces of orientation pheromones enduring for weeks at a time. Workers clear them of vegetation in order to form veritable highways along which large numbers of ants can travel easily (Hölldobler & Wilson 1990).

Trunk trails are usually dendritic in form. Each one starts from outer edge of the nest surface as a single thick pathway that splits first into branches (**Figure 1**) and then into twigs. This pattern deploys large numbers of workers rapidly into foraging areas (Hölldobler & Wilson 1990). While only a few workers drift away from the main trunk route, the majority of workers do not spread on a solitary basis until they reach the terminal twigs. Twigs and branches can be envisioned as tributaries of ant masses flowing back to the nest (Hölldobler & Wilson 1990).

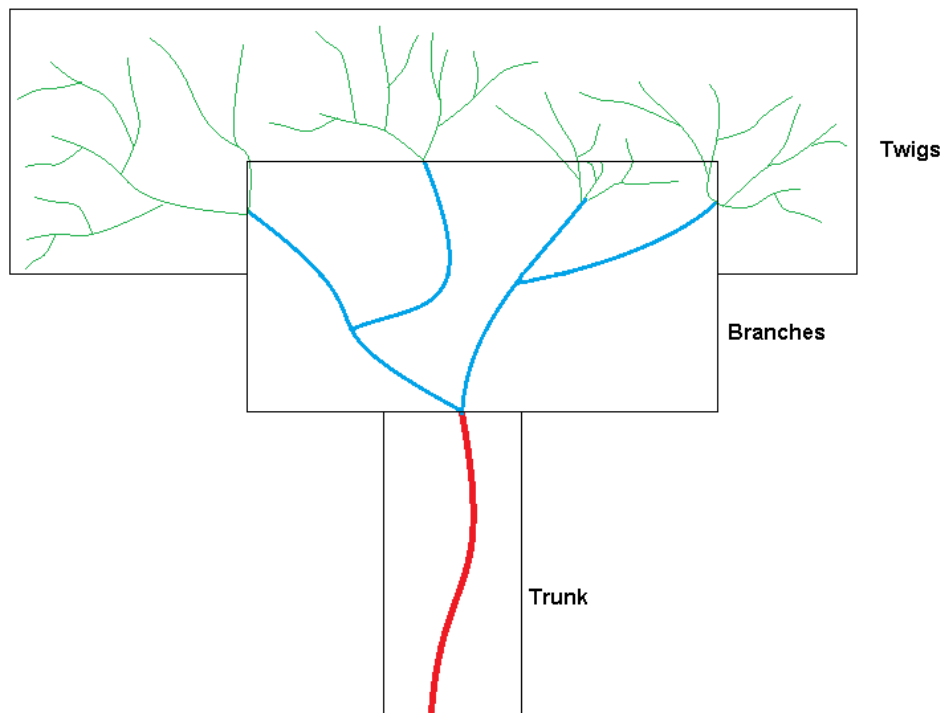


Figure 1 A schematic representation of a complete foraging trail of a harvester ant colony. Every day countless workers move out to the dendritic trails system, disperse singly and forage for food. (Modified from Hölldobler & Wilson 1990)

Size-matching and harvesting-efficiency

The third strategy is size-matching which describes the correlation between the ant body size and load size. The selection of load-size is a complex process that is influenced by various variables such as ambient temperature (Traniello *et al.* 1984), seasonality (Fowler & Robinson 1979), and food quality (Roces & Hölldobler 1994, Traniello 1989). Size-matching has not only been reported for monomorphic ant species (Davidson 1977b, Kaspari 1996) but also for polymorphic species such as harvester ants (Kaspari 1996). Rissing & Pollock (1984) hypothesized that the model of size-matching is advantageous to the ant colonies since it maximizes the colony fitness by having each of its workers' forage optimized. Furthermore, a number of authors claim that the size range of harvester ant workers represents an adjustment to align themselves to the diversity in the size of seeds and fruits (Davidson 1977b, 1978, Oster & Wilson 1978, Rissing & Pollock 1984). Thereby, harvester ants could expand their food spectrum and the possible interspecific competition could be reduced (Traniello & Beshers 1991). Moreover, it is hypothesized that size-matching increases the colonies harvesting efficiency. Harvesting efficiency can be estimated by the evaluation of the proportion of incoming loaded ants over the total number of incoming foragers (López & Haeger 1999, Solida *et al.* 2007).

3.6. Chaff piles

Brown and Lieberman (1973), Brown and Davidson (1977), Brown *et al.* (1979) and Kelrick *et al.* (1986) stated that harvester ants are very abundant in numerous habitats and are important granivores in arid systems. Food is gathered in the surrounding area of the nest and then stored

in great quantities within the nest in special chambers called “granaries”. Within these granaries, workers use their large mandibles to separate seeds from the less palatable parts and to grind seeds into ‘bread’, which is the actual year-round food (Steinberger *et al.* 1991). In this way, ant colonies can overcome periods of drought and frost seasons when seeds are scarce (Hölldobler & Wilson 1990). Plant parts, apparently not serving as food are later rejected and accumulated to chaff piles at the nest surfaces. These chaff piles represent the most of the food gathered by harvester ant colonies, both in the plant species composition and in the relative abundance of seeds of the respective plant species (Steinberger *et al.* 1991).

3.7. Predation by ant-eating spiders

Why do harvester ant colonies seem to have more different kinds of predators than other ant species? Schmidt (2016) stated, that in the habitats where harvester ants mostly occur, other prey is scarce. They live in open bare areas where they are conspicuously visible. Their vast colonies with thousands of workers provide a bounty to any predator able to exploit them. Because harvester ants are relatively large they provide nutritional potential worthy of the attention of both larger and smaller predators. Finally, harvester ant colonies persist over years at the same place. They cannot easily move the whole colony to a safer site (Schmidt 2016).

3.7.1. Adaptive shifts in behavior of ant colonies

Social insects such as ant colonies are superorganisms in which the entire colony acts much as a single organism, although one with separate mobile parts, the workers. As cells and tissues in the human body act for the good of the whole, individual workers act for the benefit of the whole colony. Workers operate to protect the queen and the rest of the colony (Schmidt 2016).

Some ant species adjust the time of main foraging activity dramatically in response to weather conditions, food availability, and the presence of foragers at any given time (Hölldobler & Wilson 1990). While in tropical habitats, daily and seasonal foraging activities of ants are strongly influenced by both temperature (Torres 1984a, b) and humidity (Levings 1983, Levings & Windsor 1984), other ant species, such as *Dolichoderus* (= *Monacis*) *bispinosus* (Olivier, 1792), have been observed to shift their foraging activities in response to invasions by competitive colonies (Swain 1977). Several other ant species have been observed to modify their nests in response to parasites or predators. For example, *Formica subsericea* Say, 1836 colonies close their nest entrances with soil, pebbles and plant material after being raided by the slave-making ant *F. subintegra* Wheeler, 1908 (Hölldobler & Wilson 1990). Additionally, traces of excavated soil and discarded cocoons, that normally litter the nest surfaces, are removed (Talbot & Kennedy 1940). *Myrmecocystus mimicus* Wheeler, 1908 colonies also close nest entrances and cover the surroundings with sand as a response to raids from neighboring colonies of the same species (Hölldobler & Wilson 1990). *Pogonomyrmex rugosus* Emery, 1895 harvester ant colonies respond to persistent attacks by the western window spider (*Latrodectus hesperus* Chamberlin & Ivie, 1935) by decreasing or entirely stopping their foraging activity and closing their nest entrances even when only 0.2 percent of the population is predated per day (MacKay 1982). Similarly, ant colonies of the desert genus *Cataglyphis* Foerster, 1850 in North Africa also close nest entrances with soil particles after being attacked by hunting spiders (Hölldobler & Wilson 1990).

3.7.2. *Exterior and interior workers*

At any given moment, only a very small proportion of workers in a typical ant colony is engaged in activities outside the nest. Inside the nest the majority of workers are inactive, grooming themselves or each other, or just running around, apparently aimlessly. Herbers (1981) pointed out in an analysis, that such apparent laziness is likely to have survival value. Under a broad spectrum of possible environmental conditions harvester ants forage, a perfectly adequate strategy is a thermostatic feeding process whereby the worker ant initiates foraging and simply continues until it reaches a certain level of acquired energy. For social insects, including ants, this rule of thumb will result in the idling of a large percentage of the population in any particular time. Yet, inactivity is a far more complicated and subtle matter in ant colonies because work is set in a social context.

What each worker does, affects not just her own physiological state but that of many others around her, in a way that strongly affects her genetic fitness.

Being largely sterile, workers are programmed to respond to the needs of the colony as a whole, even at the risk to their own lives. This broader involvement helps to explain the curiously undirected behavior of patrolling workers, whose aim can be described as inspection tour (Hölldobler & Wilson 1990). Gordon (1984, 1986, 1987) has characterized patrolling in harvester ant colonies of the genus *Pogonomyrmex* as a distinctive set of activities that include: 1) walking around outside the nest while inspecting the areal with the antennae and making more frequent stops and changes of direction than during foraging, 2) pawing at the ground with the forelegs and inspecting the resulting small depressions with the antennae, 3) standing with open mandibles at the location of disturbance. Patrollers are more likely than other labor groups to encounter threats to the colony, and they are immediately available for defense. Moreover, patrolling precedes foraging in the daily routine of undisturbed harvester ant colonies, and it appears that patrollers regularly recruit foragers to new food sources (Gordon 1983).

Masses of workers that rest or idly patrol inside the nest function as reserves. They constitute a backup for the colony in cases of emergency such as heavy rainfall which consequently flooding the nest or the invasion by a predator that requires the simultaneous engagement of numerous nest mates. Moreover, superabundance of individuals performing any given task, as for example nest construction or brood care, forces some into other, less crowded functions, and the division of labor tends to approach proportions of workers that match the needs of the colony as a whole. Many of displaced workers are searching for new tasks or at least are prepared to undertake them. They impart a flexibility to the labor schedules that allows the ant colony to adapt quickly to environmental changes (Hölldobler & Wilson 1990).

4. Aims and Objectives

4.1. Description of the nest surface and foraging trails (*Paper I, Manuscript I*)

Of several other harvester ant species, the characteristics of the nest surface and of foraging trails are well known, but not of the harvester ant species *M. wasmanni*. In the course of field work, the nest surface of mature *M. wasmanni* (**Manuscript I**) colonies and the structure of foraging trails (**Paper I**) were analyzed.

4.2. The native food spectrum

Because a comprehensive analysis of the food spectrum of the *M. wasmanni* harvester ants is not described in literature, in the present study, a qualitative and quantitative analysis of the collected propagules was performed. Furthermore, it was analyzed if the composition of the seed and fruit intake corresponds with the successive plant species' flowering periods and the resulting seed production during the observation period. Additionally, the distributional pattern of the main food resources was analyzed during the three sampling seasons in May, July/August and October 2009 (**Paper I**).

4.3. Foraging strategies

4.3.1. Size-matching and harvesting efficiency

The aspects of foraging comprising size-matching (relationships between the load ratio [mm] and ants' head width [mm]; and between the load size [mm] and ants' head width [mm]) and harvesting efficiency of *M. wasmanni* harvester ants were not investigated in past research works. Therefore size-matching and harvesting efficiency under natural conditions were investigated in the present study. Harvesting efficiency was estimated by the evaluation of the proportion of incoming loaded foragers per size class over the total number of incoming foragers per size class (López & Haeger 1999, Solida *et al.* 2007) (**Paper I**).

4.4. Chaff piles

The food spectrum of *M. wasmanni* harvester ants is not described in detail in literature. Hence, refuse pile material was collected of *M. wasmanni* colonies from the northern (Merag, Loznati), the middle (Zaglav, Belej) and the southern region (Osor, Punta Križa) of the distribution area on the Croatian island of Cres. A qualitative and quantitative analysis of the chaff pile material was performed. From the raw data, the relative frequency of plant species was calculated and finally categorized in dominance classes according to Engelmann (1978). The Jaccard Index was utilized to calculate the similarity of the plant species composition in chaff piles collected in the northern, the middle and in the southern region of the distribution area of *M. wasmanni* harvester ants on Cres.

Granivore harvester ants such as *M. wasmanni* are distinguished from the even broader group of ant species that collect seeds only because of elaiosomes, which are nutritious appendages

shaped like caps or sheaths on the seeds. Foragers discard seeds as soon as they have taken off these elaiosomes, anywhere between the plant and the nest. Resulting, these ant species are major dispersers of myrmecochorous plants. In contrast, harvester ants feed on the seeds themselves (granivory) (Hölldobler & Wilson 1990).

In this study, it was analyzed if *M. wasmanni* harvester ants could function as seed dispersers as well. They disperse plants because from time to time they discard seeds by accident on chaff piles. In this way, they compensate in part the damage caused by seed predation. Accordingly, the percentage share of viable seeds, other diaspores and plant parts of the total number of occurring propagules found in chaff piles was calculated (**Manuscript I**).

4.5. Predation impact by a myrmecophagic spider on the activity pattern of *M.*

wasmanni

The impact of predation on the activity pattern of *M. wasmanni* colonies was not investigated in past research works. It was hypothesized, that the activity patterns of *M. wasmanni* colonies are influenced not only by microclimatic conditions (Ruano *et al.* 2000, Azcárate *et al.* 2007, Cole *et al.* 2010) and interference competition (Cerdá *et al.* 1998; Bestelmeyer 2000; Sanders & Gordon 2000), but also by predation.

Nest closure by the ant colonies seems economically counterproductive compared to the lost foraging activity, although, perhaps, overall it is beneficial to the ant colonies because it is assumed that ant-eating spiders usually leave the area of inactive colonies and move to active nests nearby (Schmidt 2016). Regarding this, the relative frequency of *Z. elegans* individuals at active/inactive colonies and in chaff piles was analyzed.

With termination of aboveground foraging activity, workers started to close entrances from both the inside and outside. It was examined, whether worker ant size is related with the respective workers' behavior. Therefore, the ratio of ant size classes involved in nest closure was investigated.

M. wasmanni harvester colonies harmoniously perform complex tasks such as nest building, foraging for food, food storage, food processing, brood care, trophallaxis, and occasionally they even attack predators. It is assumed that workers can switch from one task to another, however not all transitions are possible (Gordon & Goodwin 1992, Gordon 2002). Consequently, it was examined whether perturbations such as predation by the myrmecophagous spider *Z. elegans* would affect the relative frequency of activities outside and inside the nest as well (**Paper II**).

5. Materials and Methods

In **table 1**, a short overview of the methods used in paper I, II and manuscript I is given:

Table 1 Overview of methods used in Paper I, II and in Manuscript I.

Paper/ Manuscript	Method	Description	Chapter
Paper I	The study species	<i>Messor wasmanni</i>	5.1.1.
	Study site	Fieldwork was carried out close to Zaglav.	5.2.1.
	Microclimatic measurements	Every half hour, surface temperature (°C) and surface relative humidity (% rh.) were measured.	5.2.4.
	Speed related to surface temperature	The dependency of worker speed (cm/s) subject to worker size and soil surface temperature (°C) was analyzed by a linear regression analysis.	5.2.5.
	Description of <i>M. wasmanni</i> foraging trails	The structure of foraging trails was analyzed. The mean and standard deviation were calculated for the length of pathways and branches.	5.3.
	The native food spectrum	Returning workers carrying loads were collected randomly from foraging trails.	5.4.1.
	Environmental seed availability	The environmental seed availability was assessed by averaging the quantity of seeds from 20 randomly selected seed-shedding plants per species. The calculated quantity of seeds was multiplied by the total number of plants per species occurring in five transects including a total number of twenty-five plots.	5.4.2.
	Size matching	The relationship of both between load ratio [mm] and ant head width [mm] and between load size [mm] and ant head width [mm] was analyzed using a linear regression analysis (ANOVA).	5.5.1.
	Harvesting efficiency	Harvesting efficiency was calculated by evaluating the proportion of returning loaded workers per size class over the total number of returning foragers per size class	5.5.2.
Manuscript I	Ant morphology	The head widths were measured with 0.01 mm accuracy using a Nikon stereomicroscope fitted with an ocular micrometer.	5.8.1.
	The study species	<i>Messor wasmanni</i>	5.1.1.
	Collection and analysis of chaff piles	A total number of six study sites (Merag, Loznati, Zaglav, Belej and Punta Križa) were chosen where chaff piles of <i>M. wasmanni</i> colonies were collected.	5.2.2.

	Microclimatic measurements	Six datalogger (PCE-HT71), one per study site, were utilized for microclimatic measurements (temperature [°C] and relative humidity [% rh.]).	5.2.4.
	Description of the nest surface	The average diameter (mean \pm SD) of <i>M. wasmanni</i> nest surfaces and the average distance (mean \pm SD) between nest entrance and chaff piles was calculated.	5.3.
	Analysis of chaff piles	A qualitative and quantitative analysis of the collected chaff pile material was performed. The relative frequency of plant species and diaspores was calculated from raw data and then classified in dominance classes according to Engelmann (1978).	5.6.
Paper II	Study species	<i>Messor wasmanni</i> <i>Zodarion elegans</i>	5.1.1. 5.1.2.
	The study site	Fieldwork was carried out close to Zaglav.	5.2.1.
	Microclimatic measurements	Every half hour, surface temperature and surface relative humidity were measured.	5.2.4.
	Activity pattern	It was analyzed if the activity pattern of <i>M. wasmanni</i> colonies is solely dependend on microclimatic conditions or on predation by ant-eating spiders as well. A linear regression analysis was applied to analyze the dependency of ant aboveground activity to surface temperature (°C) and surface relative humidity (%rh.).	5.7.1.
	Spider attack and nest closure	Mean and standard deviation were calculated for paralysis latency and size class distribution for workers involved in nest closure performed outside the nest.	5.7.2.
	Frequency of <i>Z. elegans</i> individuals	The relative frequency of <i>Z. elegans</i> individuals at active/inactive <i>M. wasmanni</i> harvester ant colonies and in chaff piles was recorded.	5.7.3.
	Ant morphology	The head widths between the eyes were measured with 0.01 mm accuracy using a Nikon stereomicroscope fitted with an ocular micrometer.	5.8.1.
	Culture of a <i>M. wasmanni</i> colony in the laboratory	A colony was kept in a glass terrarium with an artificial nest made of Ytong.	5.8.2.
	Culture of <i>Z. elegans</i> spiders in the laboratory	Individuals were kept in a glass tube (17 mm x 60 mm) with soil substrate at the bottom.	5.8.3.
	Perturbation experiment	The closure of nest entrances in response to predation was analyzed.	5.8.4.
	Duration of aboveground activity	A two-sample t-test was used to analyze the relationship between the duration of aboveground activity and the presence/absence of <i>Z. elegans</i> individuals.	5.8.5.

	Effect of predation on activities inside the nest	A Wilcoxon matched-pairs signed rank test was used to determine if there is an effect of spider predation on the number of workers performing specific activities inside the nest.	5.8.6.
	Marked foragers	To analyze which activities foragers perform inside the nest, workers were marked according to their body size. Observed activities were noted along with the physical size class of the marked workers.	5.8.7.

5.1. The study species

5.1.1. *Messor wasmanni*

Messor harvester ants are the most frequently appearing seed predators in the Mediterranean Basin (López *et al.* 1993, Cerdá & Retana 1994, Hensen 2002, Azcárate & Peco 2003). The subterranean *M. wasmanni* nests tend to be found in open fields and near roadsides. Nest openings are directly located onto the surface. Nests can be easily detected in the field by the clearly defined network of trunk trails and nest surfaces cleared of vegetation (Hölldobler & Wilson 1990). Granivory is characteristic of *M. wasmanni* harvester ants. Resulting, they constitute a severe source of seed mortality for many plant species, limiting their recruitment odds (Andrew 1986). Yet, occasionally, worker ants operate as vectors of dyszoochory (accidental seed dispersal) by abandoning viable seeds on foraging trails and chaff piles (Retana *et al.* 2004). Although the ants' diet is primarily composed of seeds, they occasionally feed on arthropods and snails (Traxler 2016a).

5.1.2. *Zodarion elegans*

Spiders of the genus *Zodarion* Walckenaer, 1826 occur in open, sparsely vegetated habitats from Western Europe to central Asia and were introduced to the USA (Jocqué 1991, Platnick 2014). Like many other zodariid spiders, *Z. elegans* is a medium-sized, night-active myrmecophagous spider that lives in close association with ant nests of their prey species. Individuals actively move across open ground in the evening and at night (Pekár & Křál 2001). During the day, they hide in igloo-shaped retreats covered with small sticks or pebbles, which are attached to the lower side of stones and other hard substrates (Jocqué 1991, Pekár & Křál 2001). These igloo-shaped retreats were located adjacent to ant colonies, a behavior that is likely an adaption to the open environment in which these spiders occur (Harkness 1977). Several ant-eating *Zodariid* spiders e.g. *Zodarion germanicum* (C. L. Koch, 1837) and *Z. rubidium* Simon, 1914, were found to resemble ants physically in size, colour, setosity as well as behaviourally in ant-like movement and antennal illusion (Pekár & Křál 2002). While *Z. germanicum* imitate large dark ants, such as *Formica cinerea* Mayr, 1853, *Z. rubidium* mimics red ants, e.g. *Myrmica sabuleti* Meinert, 1861 (Pekár & Křál 2002). Thus, these spiders are generalized batesian mimics. Like *Z. germanicum* and *Z. rubidium*, *Z. elegans* uses the typical "bite-and-release" prey capture tactic, which is characterized by an attacking and handling phase, followed by a waiting period at a safe distance. One advantage of this capture strategy, which limits contact between predator and prey, is that it

facilitates the predator to prevent being injured or killed when ants counter attack (Pekár 2009, Cushing & Santangelo 2002). Zodariid spiders carry the captured ant, trying to pass by approaching ants applying a special deceiving behaviour. This behavior is based on the imitation of the nestmate recognition of ants. First, by touching the curious ants' antennae with the front legs, the spider transmits a tactile cue. Second, the spider exposes the ant corpse (prey) to the ant antennates. In this manner, the dead ant corpse transmits an olfactory cue. Moreover, similar to the antennae of ants, the distal parts of the front legs of *zodariid* spiders are virtually without macrosetae. All other spider legs are covered with flattened incised setae, imitating the dense setosity of ants' extremities (Pekár & Křál 2002).

5.2. The study area

The study area was located on the Croatian island of Cres where two basic vegetation zones are present. The sub-Mediterranean (hardwood) zone includes the northern part of Cres and is made up of Downy Oak (*Quercus pubescens* Willd. 1796) and Oriental Hornbeam (*Carpinus orientalis* Mill.) forests (Rikli 1943). While the Mediterranean zone widely continues in the area from St. Blaz (the west side of the island) to Vodice and Merag (the east side of the island) and includes the southern part of the island (Galkovski 2007). The sub-Mediterranean zone is generally characterized by average lower temperatures during the winter months and of a larger quantity of average annual precipitation. The results are a shorter period of summer draught, and a winter stagnation period of vegetation (Galkovski 2007). The vegetation of the Mediterranean zone is made up of evergreen coniferous or holly oak (*Quercus ilex* L.) forests, which have by now been partially destroyed and exchanged by various other types of vegetation such as maquis, geriggué and rocky land pasturage (Rikli 1943, Horvat *et al.* 1974, Traxler 2016a). On the island of Cres *M. wasmanni* harvester ants only occur in areas with a Mediterranean vegetation and climate.

5.2.1. Study sites

For the first and third part of the thesis, fieldwork was carried out close to Zaglav (44° 48' N, 14° 21' E), a small village on the island of Cres (**Paper I, II**).

5.2.2. Collection of chaff piles (**Manuscript I**):

A total number of six study sites were chosen where chaff piles of *M. wasmanni* colonies were collected (**Figure 2**):

- 1) Study sites Ia and Ib are located in the northern zone of the distribution area of *M. wasmanni* colonies at the island of Cres:
 - Merag: sea level: 138.4 m; 44° 57' N, 14° 27' E
 - Loznati: sea level: 249.4 m; 44° 55' N, 14° 26' E

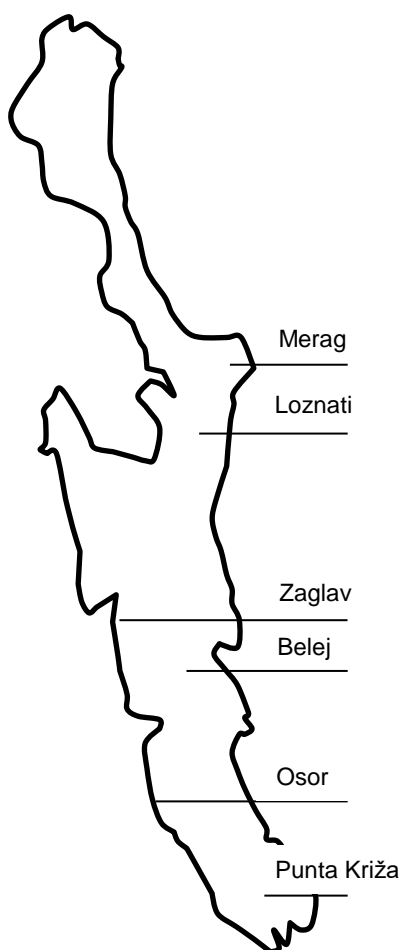


Figure 2 Geographical map of the island of Cres. The position of the study areas in the north (Merag, Loznati), in the middle (Zaglav, Belej) and in the south (S) of the distribution area of the harvester ant *M. wasmanni* on the island are marked.

In Merag, the investigated ant colonies were located along a small field path, which led up to a sheepfold. In Loznati, ant colonies were situated at the outer edge of a sheep pasture.

In Merag and Loznati, the phytogeographical characteristic carstic and pasture landscapes, including plant species such as *Juniperus oxycedrus* L., *Paliurus spina-christi* Mill., *Rhamnus intermedius* Steud. & Hochst. as well as *Stipo-salvietum officinalis* and *Festuco-koelerietum splendentis* associations, are usually exposed to the powerful action of the wind – the bora. These plant associations show gradual transitions to “garrigues”. The *Stipo-salvietum officinalis* association is widely distributed along the whole of the Croatian part of the Adriatic coast and is one of the most frequent grassland communities in the Mediterranean region. It usually develops on hill slopes on sparse soil, and constitutes a stone pasture vegetation which shows a considerable diversity of plant species, particularly under fairly extreme habitat conditions (Stančić & Pandža 2005). This association is recognisable on the basis of two characteristic plant species: *Salvia officinalis* L. and *Stipa bromoides* (L.) Dörf. The most frequent plant species in that floristic composition are: *Salvia officinalis* L., *Bromus erectus* Huds., *Helichrysum italicum* (Roth) G. Don, *Brachypodium retusum* (Pers.) P. Beauv. 1812, *Aethionema saxatile* (L.) W. T. Aiton, *Teucrium montanum* L., *Asparagus acutifolius* L., and *Dactylis glomerata* L. subsp. *Hispanica* (Roth) Nyman (Stančić & Pandža 2005). On pastures, nitrophilous species such as *Scolymo-marrubietum incanae* associations are frequently found (Gazi-Baskova 1975).

2) Study sites IIa and IIb are located in the middle of the distribution zone:

- Zaglav: sea level: 6.5 m; 44° 48' N, 14° 21' E
- Belej: sea level: 132.4m; 44° 46' N, 14° 25' E

In Zaglav, a *Stipo-salvietum officinalis* association was found. Ant colonies were situated along a small field path leading down to the sea. The vast grass lands near Belej belong to plant communities such as *Brachypodio-chrysopogenetea* which are rich in species of the plant families Asteraceae and Fabaceae (Gazi-Baskova 1975), and the *Festuco-koelerietum splendentis* association what can be linked to areas which are relatively less degraded (Stančić & Pandža 2005).

3) Study sites IIIa and IIIb are located in the south of the distribution zone:

- Punta Križa: sea level: 40.0 m; 44° 41' N, 14° 23' E
- Osor: sea level: 0.0m; 44° 39' N, 14° 28' E

In Osor, ant colonies were located close to the sea. The azonal Mediterranean salt marsh ecosystems of Osor are dominated by *Juncetea-maritime* and *Arthrocnemetea* associations in close proximity to the sea, while in elevated areas where seawater is considerably freshened by rain *Nanojuncetea* associations are present (Martinoli 1948). Ant colonies in Punta Križa were situated on a sheep pasture, characterized by the occurrence of nitrophilous species such as *Scolymo-marrubietum incanae* associations (personal observation).

5.2.3. Statistics

For the statistical analysis of the data, the softwares SPSS Statistics 23 and Graph Pad Prism 5 were used, with a significance level of $p < 0.05$. All statistical tests were two-tailed.

5.2.4. Microclimatic measurements

In **Paper I**, it was evaluated if worker running speed depends on worker size and soil surface temperature. In **Paper II** it was focused on the activity pattern of *M. wasmanni* colonies, which is affected by both, the microclimatic conditions (Ruano *et al.* 2000, Azcárate *et al.* 2007, Cole *et al.* 2010) and by predation (Traxler 2016b).

Microclimatic conditions were measured in May 2008 and May, August and October 2009 for five consecutive days. Data collection started at 04:30 AM in the morning before the colonies were active outside the nest. Measurements continued during the activity period and were completed at 22:30 PM, when the colonies ceased aboveground activity. Surface temperature and surface relative humidity were measured every 30 minutes. For all investigated colonies, a PT 100 Testoterm 0.1°C precision thermometer and a PT 100 Testoterm 0.1% precision thermohygrometer were used. All measurements were taken at a distance of 10 cm from the nest entrances. Sensors were protected from direct sun radiation (**Figure 3**). On the whole, six colonies in May 2008, eight colonies in May 2009, five colonies in August 2009, and three colonies in October 2009 have been observed (**Paper I, II**). Each *M. wasmanni* colony was evaluated only once during field studies to avoid repeated data taking.

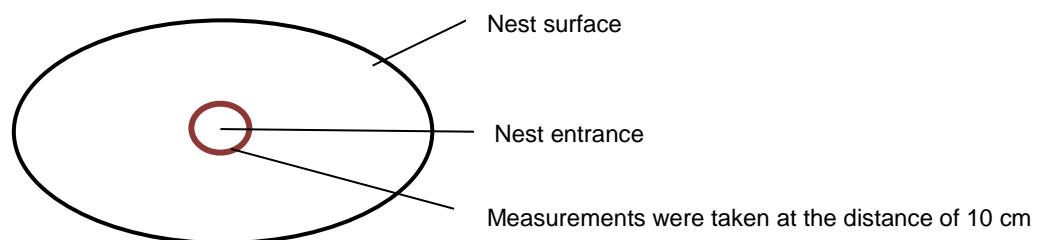


Figure 3 Distance at within measurements were taken around the nest entrance.

Six dataloggers (PCE-HT71), one per study site, were utilized for microclimatic measurements (temperature and relative humidity): Merag, Loznati, Zaglav, Belej, Osor and Punta Križa. All dataloggers were fixed on the soil surface for the duration from 28th May 2009 to 24th October 2009. Both dataloggers from Osor and Punta Križa have been damaged, resulting data therefrom could not be read (**Manuscript I**).

5.2.5. Speed related to surface temperature

Throughout the time of aboveground activity, worker speed was measured as the time period, which is required to cover a distance of 20 cm along foraging trails. Because worker speed is temperature- and size-dependent (Rissing 1982), worker speed was determined for unloaded and loaded returning workers as a function of soil temperature and worker ant size.

Data analysis: The dependency of worker speed (cm/s) subject to worker size and soil surface temperature (°C) was assessed by a linear regression analysis. The dependent variable was worker speed, and the independent variable was soil surface temperature (**Paper I**).

5.3. Description of *M. wasmanni* nest surfaces and foraging trails

M. wasmanni harvester ant colonies construct subterranean nests. Nest surfaces are completely free of ground-covering vegetation and chaff piles are located at the outer edge of the nest surfaces. The widest diameter from nest surfaces and the distance between the nest entrances and chaff piles were taken from 35 colonies.

Data analysis: The average diameter (mean \pm SD) of *M. wasmanni* nest surfaces and the average distance (mean \pm SD) between nest entrance and chaff piles were calculated; N = 35 (**Manuscript I**).

The structure of foraging trails was analyzed. Each trail arises as a single broad pathway near the nest, then diverges first into branches and finally into twigs. The total length of pathways (N = 39) and branches (N = 42) was taken.

Data analysis: The mean and standard deviation were calculated for the length of pathways and branches (**Paper I**).

5.4. The food spectrum of *M. wasmanni* harvester ants

5.4.1. The native food spectrum

During aboveground activity, returning workers carrying loads were collected randomly from foraging trails at a distance of 10 cm from the nest entrances (**Figure 4**). Loaded workers were conserved in individual vials containing 70% ethyl alcohol. Unloaded workers were collected as well to ensure not to miss workers carrying smaller loads. The analysis of workers and their loads was performed in the laboratory. If possible, loads e.g. seeds, fruits, other plant parts and animal remains as well were classified to species or genus level and any items that were not seeds were noted. The minimum distance between sampled *M. wasmanni* colonies was 50 m (**Paper I**).

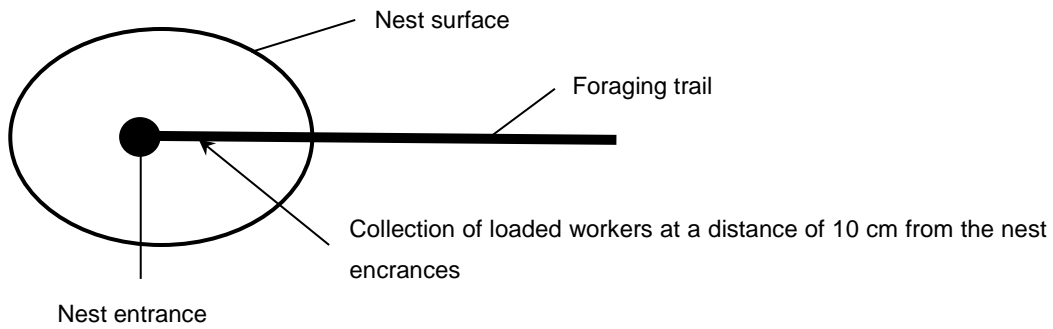


Figure 4 Description of the sampling position.

5.4.2. Environmental seed availability

The environmental seed availability was assessed by averaging the quantity of seeds from 20 randomly selected seed-shedding plants per species (Whitford 1978, Nicolai *et al.* 2007). This calculated quantity of seeds was multiplied by the total number of plants per species, which occurred in 25 plots during sampling periods in May 2009, July/August 2009 and October 2009. Five 25 X 25 cm plots, at a distance of 5 m from each other, were set along five transects, each one of 25 m (**Figure 5**). These five transects were arranged radially around *M. wasmanni* harvester ant colonies. That number of seeds per plant species (mean number of seeds x total number of plants per species) was considered as an overall estimate of the environmental seed availability per season (Davidson 1977a). Unfortunately, due to aridity during the summer months, it was not possible to collect collected plants as well as seeds in two out of three sampling seasons (July/August and October). Resulting, all data were excluded from the analysis (**Paper I**).

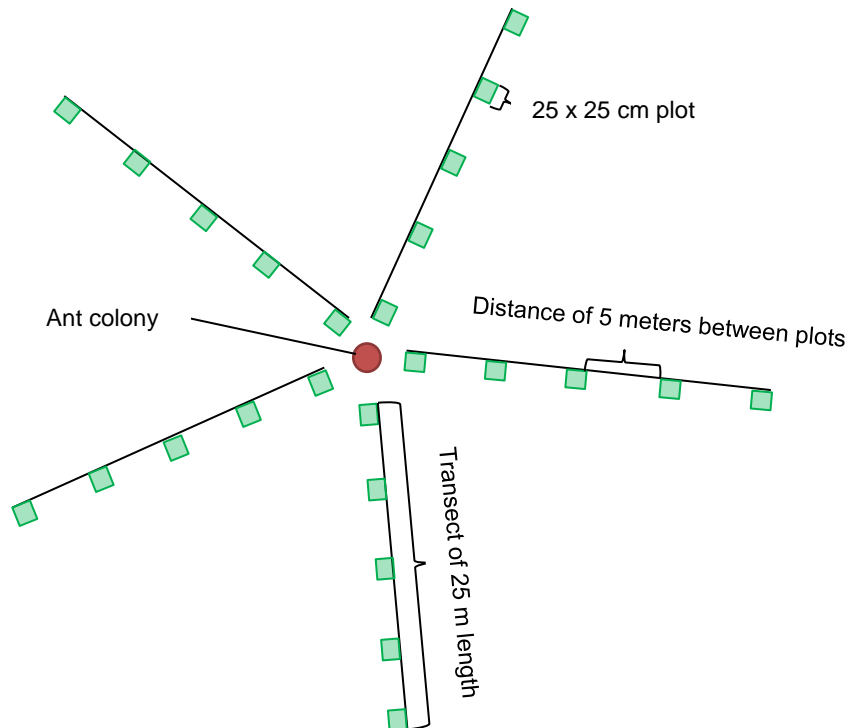


Figure 5 Radially arrangement of transects around *M. wasmanni* colonies.

5.5. Foraging for food

5.5.1. Size matching

To test the hypothesis which predicts size-matching (Rissing & Pollock 1984), a total of seven hundred seventy-six loaded workers, returning to the nest along foraging trails, were randomly collected at a distance of 10 cm from the nest entrances (**Figure 4**). Each worker and its load were retained in 70 % ethyl alcohol. The load ratio was calculated as the sum of ant head width and load size divided by the ant head width. Measurements of load size and worker ant head width were recorded using a Nikon stereomicroscope fitted with an ocular micrometre. Measurements were performed with 0.01 mm accuracy.

Data analysis: The relationships between load ratio [mm] and ants' head width [mm] and between load size and ants' head width [mm] were analyzed using linear regression analysis (ANOVA). The load ratio was calculated as follows: (ant size + load size)/ant size (**Paper I**).

5.5.2. Harvesting efficiency

Because *M. wasmanni* workers display slight allometry with continuous size variation, three distinct worker size-classes (minor-, media- and major-workers) were introduced.

Data analysis: Harvesting efficiency was calculated by evaluating the proportion of returning loaded workers per size class over the total number of returning foragers per size class (**Paper I**). Two arbitrary 1-min flow counts were carried out daily in periods of 30 minutes between 07.00 A.M. and 10.00 A.M during the study periods. The averaged value of two counts per counting period provided an estimate of the harvesting efficiency per worker size class. To analyse, if harvesting efficiency increases as a function of colony activity, the percentage of loaded ants per size class was correlated with flows of incoming ants per size class using a Pearson correlation (Graph Pad Prism).

5.6. Analysis of chaff piles

In October 2009 chaff piles that accumulated since the end of the hibernation in spring were collected. In early spring, prior to the end of hibernation, old chaff piles were removed from the nest surfaces. Using a Mettler MP 4600 scale, the fresh weight of chaff piles was determined. For the qualitative and quantitative analysis of the plant species composition of the chaff pile material, chaff piles of thirty nests were collected; five samples per study site (Merag, Loznati, Zaglav, Belej, Osor, Punta Križa). Per nest 100 g chaff pile material was taken, making a total sum of three kilos to analyze. If possible, occurring seeds, diaspores, other plant fragments and animal fragments were determined to genus or species level (**Manuscript I**).

Data analysis: To compare the fresh weight of chaff piles of *M. wasmanni* colonies from the north (Merag, Loznati), the middle (Zaglav, Belej) and the south (Osor, Punta Križa) of the distribution area on the island Cres average weight and the standard deviation (mean \pm SD) were calculated (N = 30). The relative frequency of plant families, plant species and diaspores was calculated

from raw data and then classified in dominance classes according to Engelmann (1978) (**Table 2**). Following formula was applied:

$$D = \frac{\text{Number of individuals per family/species } i \times 100}{\text{Total number of individuals of all species}}$$

Dominance class	% of individuals	Classification
eudominant	32 – 100	main species
dominant	10 – 31.9	main species
subdominant	3.2 – 9.9	main species
recedent	1.0 – 3.1	companion species
subrecedent	0.33 – 0.99	companion species
sporadic	< 0.32	companion species

Table 2 Classification into dominance classes according to Engelmann (1978).

For the analysis of the diversity of chaff piles the diversity index according to Shannon-Weaver (H'), the maximal diversity (H_{max}) and the Evenness (E) were calculated. The Jaccard Index is used for comparing the similarity of chaff pile samples collected in the north (Merag, Loznati), in the middle (Zaglav, Belej) and in the south (Osor, Punta Križa) of the distribution area of *M. wasmanni* harvester ant colonies on the island of Cres.

5.7. The temporal activity pattern related to the presence of predators

5.7.1. Activity pattern

The impact of both, the microclimatic conditions (Ruano *et al.* 2000, Azcárate *et al.* 2007, Cole *et al.* 2010) and the presence of predators i.e. *Z. elegans* spiders, on the daily activity pattern of *M. wasmanni* colonies was investigated. Every 30 minutes the number of *M. wasmanni* workers leaving and returning to the nest was recorded for a time period of one minute. Simultaneously, the microclimatic conditions (surface temperature and relative humidity) and the presence of ant-eating spiders were recorded.

Data analysis: A linear regression analysis was applied to analyze the dependency of ant aboveground activity to surface temperature and surface relative humidity from May 2009 to October 2009. In all analyses, the dependent variable was the number of workers leaving the nest, and the two independent variables were soil temperature and relative humidity (**Paper II**).

5.7.2. Spider attack and nest closure

With termination of aboveground activity, the duration of nest closure was documented. The presence of different worker size led to an examination of whether the phenomenon of polyethism was evident. Resulting, the worker ant size (major-, media- and minor-sized workers) was taken into account in the procedure of nest closure. The number of collaborating workers was recorded at 10-min intervals.

Data analysis: Mean and standard deviation (mean \pm SD; N = 6) were calculated for paralysis latency and size class distribution for workers involved in nest closure performed outside the nest (**Paper II**).

5.7.3. Frequency of *Z. elegans*

The relative frequency of *Z. elegans* individuals at active/inactive *M. wasmanni* harvester ant colonies and in chaff piles was recorded in May, August and October 2009. Nine active and seven inactive colonies in May 2009, nine active and eight inactive colonies in August 2009 and nine active and six inactive colonies in October 2009 have been analyzed. Colonies were included in the field studies only once to avoid repeated measurements.

Data analysis: The relative frequency of *Z. elegans* individuals found within a distance of max. 0.5 m to active/inactive ant colonies was compared with an unpaired t-test (**Paper II**).

5.8. Laboratory investigation

5.8.1. Ant morphology

Worker ant head widths [mm] were used to assess the presence of physically distinct size classes (Wilson 1953). Ants were measured across the eyes in order to determine the average head widths. The head widths were measured with 0.01 mm accuracy using a Nikon stereomicroscope fitted with an ocular micrometer. Per colony, a sample of 50 workers per size class (minor, media and major workers) was taken. Ten colonies were observed (**Paper I**). Thirty workers per size class were taken from the laboratory colony after experiments were completed (**Paper II**). A one-way analysis of variance was applied to analyze size differences in the worker caste (**Paper I, III**).

5.8.2. Culture of a *M. wasmanni* colony in the laboratory

Hölldobler & Wilson (1990) proposed that, for close behavioral studies, more elaborate artificial nests are required. For many years, they used an economical arrangement that serves for both mass culturing and behavioral observation of a majority of ant species. Hence, for the present study, a *M. wasmanni* harvester ant colony was cultivated in the laboratory following the instructions of Hölldobler & Wilson (1990). A newly collected *M. wasmanni* ant colony consisting of a single queen, workers as well as preimaginal stages such as larvae and eggs was brought into the laboratory and placed into a glass terrarium in which previously an artificial nest made of Ytong was placed. Nine chambers were caved into the Ytong that were roughly similar in size and proportion to the natural nest chambers of a *M. wasmanni* colony (**Figure 6**). In *M. wasmanni*

colonies, chambers are typically ovoid or circular in shape and 1 – 6 centimeters across; hence chambers should be excavated that are about 4 – 6 centimeters wide and 1 centimeter deep. The artificial chambers were connected by galleries which a diameter of 5 millimeters. For the purpose of moisture supply, one additional chamber was excavated and filled with a sponge. A sealable opening was affixed, to be able to fill in water for the purpose of moistening the Ytong and because ants should not have access to this chamber. Additionally, in a cylindrical bore a sealable tube was introduced for measurements of the relative humidity within the Ytongnest without disturbing the colony. Measurements of the relative humidity were performed using a PT 100 Testoterm 0.1% precision thermohygrometer (**Paper II**).

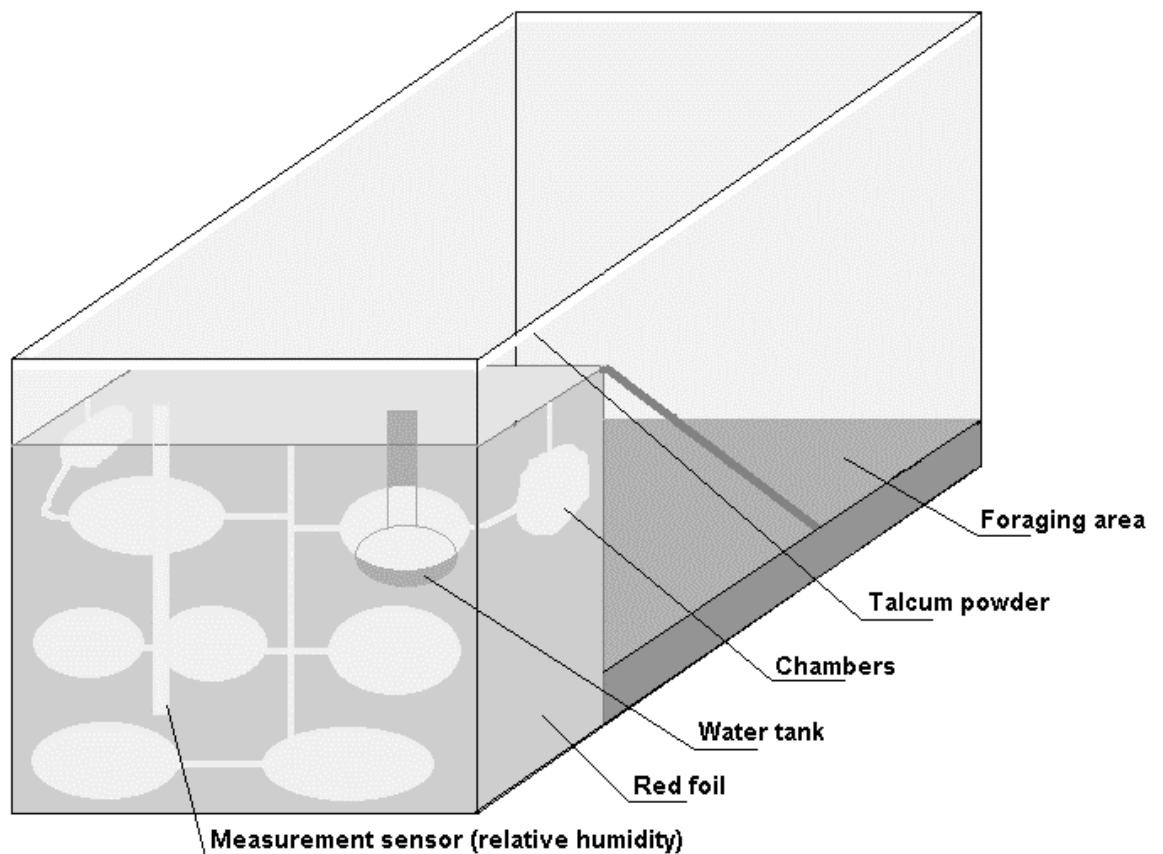


Figure 6 The schematic representation of the formicarium in which a *M. wasmanni* colony fragment was kept in the laboratory.

Because ants are unable to perceive red light, the glass panes through which the workers were visible in the formicarium were covered with red foil. The colony was kept permanently in an Ytong nest with a foraging area at a room temperature of $23 \pm 3^\circ\text{C}$, a relative humidity of 60%, and under a constant photoperiod cycle of 12:12 h. The formicarium was covered with gauze to prevent ants from escaping. The colony was regularly fed a solution of brown sugar (1 M), mixed seeds (mainly canary grass and oats) and twice a week on dead cockroaches (*Periplaneta Americana* [Linnaeus, 1758]). All experiments were conducted in the same formicarium.

5.8.3. Culture of *Z. elegans* spiders in the laboratory

Additionally, ten mature *Z. elegans* individuals were collected by hand in close vicinity to Martinšćica (44° 49' N, 14° 21' E). Spiders in the genus *Zodarion* occur in open, sparsely vegetated habitats from Western Europe, Mediterranean, Middle East to Central Asia and were introduced to the USA (Jocqué 1991, Platnick 2014). In the laboratory, each spider was put in a glass tube (17 mm x 60 mm) with soil substrate at the bottom. The substrate was moistened every third day with a drop of water. The dishes were kept at room temperature $23 \pm 3^{\circ}\text{C}$ under a constant photoperiod cycle of 12:12 h. Spiders were fed with a single *M. wasmanni* worker ant (medium-sized) regularly at four-day intervals for a period of two months (from August to the end of September). Dead ant remains were removed from the tubes 1 day after feeding (**Paper II**).

5.8.4. Perturbation experiment: closure of nest entrances in response to predation

To avoid a possible saturation effect on the predatory behavior of *Z. elegans* individuals, the spiders were starved for at least eight days prior to the experiments. During captivity, most of the spiders built igloo-shaped retreats. Prior to the experiments, the spider that was used for the trial was prompted out of its retreat using a fine brush and then released into the formicarium. If the spider did not capture an ant within the first 15 min, the experiment was terminated and the spider was placed back into its glass vial. In case of a capture, the spider remained in the formicarium for at least 20 days. In case of a repeated capture, the experiment was prolonged up to 30 days. A total number of four perturbation experiments were carried out (**Paper II**).

5.8.5. Duration of aboveground activity

The relationship between the duration of aboveground activity (h/day) of *M. wasmanni* workers and the presence/absence of *Z. elegans* individuals was analyzed using a two-sample t-test.

5.8.6. Effect of predation on activities inside the nest

Following Hölldobler & Wilson (1990), the quantity of behavioral acts recorded during the counts was used as sample size (N). The traced activities inside the nest are listed in **Table 1 of Paper II**. Observations commenced on the first day after the closure of nest entrances. In total, nine chambers were monitored per count. All observed activities were noted along with the worker size (minor-, media- and major-worker). Counts were performed in an interval of two hours throughout the day, yielding a total number of twelve counts per day. During the count, the whole laboratory was darkened. Because ants are unable to perceive red light, the glass panes through which the workers were visible in the individual chambers were covered with red foil. Additionally, red light was used during the counts (**Paper II**).

In the course of the four experiments, entrances remained closed between two and six days (**Table 2 of Paper II**). The analyses included three of the four experiments, based on the assumption that the effect of predation increases the longer the entrances remained closed. Per included experiment, counts were performed at three consecutive days, yielding a total number of nine observation days. For the purpose of a comparison between the behavior of an ant colony

under disturbed conditions (predator is present in the formicarium) and under undisturbed conditions (predator is not present in the formicarium), the same observation procedure was repeated, but without a predator in the formicarium. Under undisturbed conditions, behavioral acts were recorded for 30 days.

Data analysis: for each activity listed in **Table 1 of Paper II**, the following calculation was performed: to calculate the average value per day, the total number of times a certain activity was performed per physical size class during the observation period was divided by the number of observation days (nine days under disturbed conditions, 30 days under undisturbed conditions). Then, the average value per day was divided by the percentage share of the respective size class (major-, media-, minor-workers) in the laboratory colony. That ant colony consisted of 6% major-workers, 18% medium-workers and 76% minor-workers. Subsequently, a Wilcoxon matched-pairs signed rank test was applied as a non-parametric test to determine if there is an effect of spider predation on the number of workers performing specific activities inside the nest. A non-parametric test was used because normality could not be assumed (**Paper II**).

5.8.7. Marked foragers

Prior to each perturbation experiment, 10 loaded foragers per physical size class returning to the nest along the foraging trail were collected. These workers were marked with a waterproof touch-up stick. Within two hours, they were thereafter returned to the formicarium. Each of the three physical size classes was assigned a unique color of paint. Resulting, workers were marked according to their size. Investigations started on the first day after nest entrances were closed. Once more, every observed activity was noted along with the physical size class of the marked worker. At two-hour intervals, observations were performed throughout the day, yielding a total of 12 observations per day. After termination of the experiments, only 3-4 out of 10 minor-workers, 4-5 out of 10 medium-workers and 2-3 out of 10 major-workers were still alive (**Paper II**).

6. Results

6.1. Paper I

Traxler T. (2016) Native food spectrum, size-matching and foraging efficiency of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae). *Ecologica Montenegrina*, 7: 451-463.



Foto by T. Traxler

Native food spectrum, size-matching and foraging efficiency of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae)

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Abstract

This study examined the food spectrum, size-matching and harvesting efficiency of the Mediterranean harvester ant *Messor wasmanni* Krausse, 1910, a major seed predator on annual grasslands, on the Croatian island of Cres. The ant workers collect available food items not only from the soil surface (post-dispersal seed predation), but also directly from the mother plant (pre-dispersal seed predation). The distributional pattern of the main food resources therefore changed constantly from May to October 2009. This investigation shows that food items were collected either from several distinct small regions, or from widely distributed zones of the foraging ground. Accordingly, the foraging strategies are a mixture of individual foraging and column foraging, adjusted to the ants' needs. Moreover, under natural conditions, *M. wasmanni* workers do not show size-matching at foraging trails. Little, if any, size variation of harvested seeds and fruits can be attributed to the foragers' body size. Small workers did not appear to be constrained by load size, which indicates that size-matching may not be an adequate measure of colony foraging success for *M. wasmanni*. I further observed that the harvesting efficiency of media- and major-sized workers decreased considerably from May to October 2009, whereas the harvesting efficiency of minor-sized workers constantly increased over the year. This finding suggests that the worker size and the resulting difference in individual metabolism play an important role for the harvesting efficiency of *M. wasmanni*.

Key words: harvester ants, size matching, food spectrum, harvesting efficiency, granivory.

Introduction

The Mediterranean harvester ant *Messor wasmanni* Krausse, 1910 is a common seed predator on Mediterranean grasslands across southern Europe. Several studies revealed that granivory is a feature common to the whole *Messor* Forel, 1890 genus (Hahn & Maschwitz 1985, Hobbs 1985, Reyes-López & Fernández-Haeger 2002). Typically, *M. wasmanni* workers collect food items, such as fruits and seeds, and store them in specific chambers within their nest. Within these chambers, metapleural glandular secretion prevents seed germination and decomposition by mushrooms and bacteria (Schildknecht & Koob 1971, Celli & Maccagnani 1994). This strategy helps the ants to preserve food items and to overcome periods of inactivity outside the nest and low seed production (Schildknecht & Koob 1971, Celli & Maccagnani 1994).

Within a *M. wasmanni* colony, the sterile worker force shows allometric growth (Solida *et al.* 2007). This polymorphism is defined as the occurrence of more than one form or type of individuals among members of a single species, e.g., numerous ant species exhibit growth over a sufficient range to produce individuals of different sizes, body proportions, or both (Wilson 1953). Accordingly, the ant workers' size

represents a limit for the quantity and quality of tasks an individual worker can perform in connection with colony life. Polymorphism also encompasses cooperative behavior among colony members (Brian 1979).

Several authors hypothesize that the model of size-matching (the pairing of worker size and carried load size) is advantageous to the colony because it maximizes colony fitness by optimizing the foraging of each of its workers (Rissing & Pollock 1984). This increases the colony's foraging efficiency (López & Haeger 1999, Solida *et al.* 2007). A harvester ant species with a slightly polymorphic worker caste like *M. wasmanni* may optimize the collection of food items by delegating the task of carrying larger loads to larger workers and smaller loads to smaller workers. Furthermore, several authors claim that the size range of workers of harvester ants is a specific adaptation to match the predicted size variability in seeds and fruits (Davidson 1977, 1978, Oster & Wilson 1978, Rissing & Pollock 1984). Based on this assumption, the food spectrum can be expanded and the interspecific competition can potentially be reduced (Traniello & Beshers 1991). An increasing selectivity with distance from the nest was confirmed in *Pogonomyrmex barbatus* Smith, 1858 (Davidson 1978) and *P. occidentalis* (Cresson, 1865) (Crist & MacMahon 1992). In contrast, similar experiments on *Veromessor* Forel, 1917 and *Messor* Forel, 1890 harvester ants (Rissing & Pollock 1984, Baroni-Urbani & Nielsen 1990) and on *Pogonomyrmex badius* (Latreille, 1802) (Ferster & Traniello 1995) failed to show any significant change in the size range of collected food items with different foraging distances. Most of the studies that focus on aspects of foraging in ants, however, were conducted on harvester ant species occurring in the North American desert and semi-arid environments. Furthermore, experiments were carried out under laboratory or semi-natural conditions using baits of non-native seeds (Crist & MacMahon 1992). Although artificial seeds help control for food availability, such studies distort reality by recreating oversimplified environments (Detrain *et al.* 2000).

The present study investigates the harvesting behavior of the Mediterranean harvester ant *Messor wasmanni* under natural conditions with real seed availability. It is assumed that the ant colonies are able to maximize the acquisition of food resources by both (a) fitting the spatial distribution of foragers with the distribution of food items and (b) adapting foraging behavior to environmental conditions. Accordingly, the main objectives of the present study are to analyze: 1) the temporal predation pattern in relation to the native food spectrum, and 2) the aspects of foraging comprising size-matching and harvesting efficiency under natural conditions.

Materials and Methods

Study area and study organism

The western and southern areas of the Island of Cres are subject to a Mediterranean climate. Two basic vegetation zones are present on the island. The northern part is characterized by the sub-Mediterranean (hardwood) type with deciduous forests (Horvat *et al.* 1974, Traxler 2016a). The southern part is of the Mediterranean (evergreen) vegetation type, which includes evergreen Holm Oak woods, whereas Downy Oak and Oriental Hornbeam woods are present in the north (Horvat *et al.* 1974, Traxler 2016a).

The harvester ant *Messor wasmanni* is a common seed predator in the Mediterranean grasslands with the distribution from Italy to the Balkan Peninsula and Turkey (Bračko *et al.* 2014). The nests can be easily detected in the field through the clearly defined network of trunk trails (Hölldobler & Wilson 1990). The ant's diet is primarily composed of seeds and other plant parts (e.g., leaves, flower parts), insects and the parts, as well as snails (personal observation).

Study site

The field work was carried out close to Zaglav, a small village on the Island of Cres (44° 48' 21.1" N, 14° 21' 53.2" E). Microclimatic measurements and flow counts of both, returning and departing workers from the nest were performed between 28.05-30.05.2009, 30.07-01.08.2009 and 29.10-31.10.2009. In half-h periods, returning and departing ants from the nests were sequentially recorded by counting throughout the day between 04:30 AM and 22:30 PM. Five colonies in May 2009, two colonies in July-August 2009 and three colonies in October 2009 have been observed. To avoid repeated measurements, each colony was evaluated only once during the field studies. Each observation took place and was recorded on a different day.

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Microclimatic measurements

Surface temperature and surface relative humidity measurements were performed for all investigated colonies each half-h using a PT 100 Testoterm 0.1°C precision thermometer and a PT 100 Testoterm 0.1% precision thermohygrometer. All measurements were taken close to the nest entrances in a radius of max. 10 cm. The first measurements were taken in the morning before the colonies became active. Continuous measurements were performed during the activity period of the colonies. Measurements were completed when the colonies ceased activity. As a precaution, the sensors were protected from direct Sun radiation.

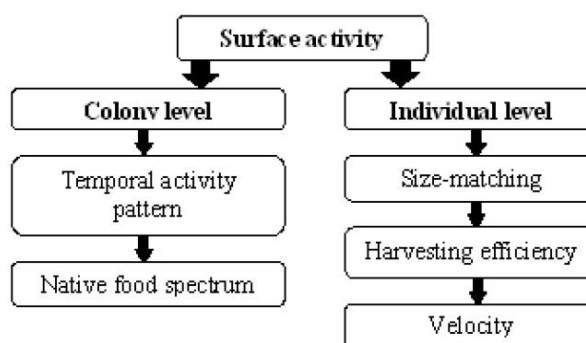


Figure. 1. Overview of the topics discussed in the paper. Surface activity was analysed at both colony level and individual level.

Surface activity at colony level*Temporal activity pattern*

The number of *M. wasmanni* workers departing and returning to the nests was recorded. Two 1-min flow counts of both returning and departing workers were carried out in half-h periods. The average values of entries and exits of each section were defined as the activity index (Fig. 1).

The native food spectrum

During periods of aboveground activity, returning foragers carrying food items and other materials were collected randomly from foraging trails at a distance of 10 cm from the nest entrances (Fig. 1). Loaded ants were picked up with forceps and retained in individual vials containing 70% Ethyl alcohol for further analysis in the laboratory. Unloaded ants were periodically collected to ensure not to miss ants carrying smaller items. Seeds were classified in the laboratory and any items that were not seeds were noted. The length of each foraging trail was measured. The minimum distance between sampled ant colonies was 50 m.

Environmental seed availability

The environmental seed availability in the study area was estimated by averaging the number of seeds from 20 randomly selected seed-shedding plants per species (Whitford 1978, Nicolai *et al.* 2007). This calculated number of seeds was multiplied by the total number of plants per species recorded in twenty-five 25 x 25 cm plots during sampling periods in May, July-August and October 2009. Five plots, at a distance of 5 m from each other, were set along five transects of 25 m each, arranged radial around ant colonies. This number of seeds per species (mean number of seeds x total number of plants per species) was considered as an overall estimate of the environmental seed availability per season (Davidson 1977). Unfortunately, due to aridity in the summer months, it was not possible to collect seeds from the sampling sites and from the plants in two out of three sampling seasons (July-August and October 2009). These data were excluded from the analysis.

Surface activity at individual level*Morphology*

Morphological dynamics related to the respective workers' behaviour was examined by measuring the head

width of small-, media- and large-sized workers. Ants were measured across the eyes to determine the average head widths. The head widths were measured with 0.01 mm accuracy using a Nikon SMZ745 stereomicroscope fitted with an ocular micrometer. Head widths were obtained to assess the presence of physically distinct size classes (Wilson 1953). Per colony, a sample of 50 workers per size class (small-, media- and large-sized workers) was taken. Ten colonies were observed.

Size matching

To test the hypothesis that predicts size-matching, loaded ants, returning to the nests along foraging trails, were collected 10 cm far from the nest entrances (Fig. 1).

The relationship between load ratio and ant size classes was investigated. The load ratio was calculated as the sum of ant head width + load size divided by the ant head width. Seven hundred seventy six random loaded ants, returning to the nest at foraging trails, were collected at a distance of 10 cm from the nest entrances. Each ant and its load were retained in 70% Ethyl alcohol. Many of the seed-looking loads carried by workers were actually fruits because structures that associate with the pericarp or the inflorescence may remain attached to the seed after dispersal. The term “load” is therefore used rather than “seed” to avoid confusion. Measurements of load size (maximum length) and worker ant head width were recorded using a Nikon SMZ745 stereomicroscope fitted with an ocular micrometer. The head width and the load size (maximum length) were measured with 0.01 mm accuracy.

Harvesting efficiency

Messor wasmanni exhibits size polymorphism. Three distinct worker size classes, i.e., minor-, media- and major-sized, were therefore introduced. Measurements were carried out daily between 07:00 AM and 10:00 AM during the study periods. Two arbitrary 1-min flow counts, referred to as the counting periods of returning loaded and unloaded workers, were performed each half h. Workers within a counting period were then assigned to one of the three size classes for data evaluation. The average values of a counting period provided a measure of the daily harvesting activity per size class. Harvesting efficiency was estimated by evaluating the proportion of incoming loaded ants per size class over the total number of incoming foragers per size class (Fig. 1).

Speed related to surface temperature

Worker speed was assessed as the time required covering 20 cm along foraging trails throughout the time of activity. Worker speed was determined for unloaded and loaded returning workers. Worker speed is temperature- and size-dependent (Rissing 1982); therefore, worker size classes were evaluated separately (Fig. 1).

Statistics

For the statistical analysis of the data, the softwares SPSS Statistics 23 and Graph Pad Prism 5 was used, with a significance level of $p < 0.05$. A one-way analysis of variance was applied to analyze size differences in the worker caste. All statistical tests were two-tailed. The relationship of both between load ratio and ant size and between load size and ant size was analyzed using linear regression analysis (ANOVA). The load ratio was calculated as follows: $\text{ant size} + \text{load size} / \text{ant size}$. The dependency of worker speed subject to worker size and soil surface temperature was analyzed by linear regression analysis. Worker speed (cm/s) as a function of soil surface temperature ($^{\circ}\text{C}$). The dependent variable was worker speed, and the independent variable was soil surface temperature. The percentage of loaded ants was correlated with flows of incoming ants using a Pearson correlation (Graph Pad Prism).

Results

Surface activity at the colony level

The native food spectrum

Messor wasmanni forms narrow, cleared trunk trails, which in the present study reached a total length of up to 26.7 m, along which workers move. These trunk trails are typically dendritic in their form and are used for foraging. Each trail arises as a single broad pathway (length: $3.82 \text{ m} \pm 3.00 \text{ m}$, mean \pm SD, $n = 39$) near the

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nest, then diverges first into branches (length: $1.89 \text{ m} \pm 3.03 \text{ m}$, mean \pm SD, $n = 42$) and finally into twigs. These terminal twigs shift from day to day, whereas trunks and branches persist over months.

The survey of the composition of the food items gathered by *M. wasmanni* workers involved taking samples from foragers returning to the nest for three days per sampling season in May, July-August and October 2009. Approximately 3,700 objects were identified. Three categories of gathered objects were found: 1) seeds, fruits and vegetative plant parts such as leaves, stems, parts of flowers other than seeds and fruits; 2) whole arthropods or the parts, faeces, snail shells and living gastropods; 3) small stones and particles of soil.

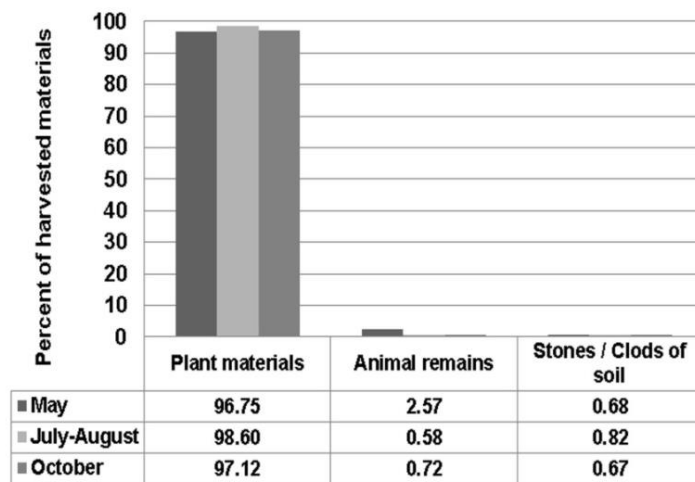


Figure 2. Frequency distribution of harvested material in percent (May, July-August and October 2009). During periods of aboveground activity, returning foragers carrying food items and other materials were collected at random from foraging trails 10 cm far from the nest entrances.

Plant material represented the vast majority (max. 97.5%) of harvested material in all sampled seasons. Workers collected available seeds, fruits and other plant materials such as green leaves and flower petals not only from the soil surface, but also directly from the mother plant. Plants affected by the latter behaviour included the species *Asparagus acutifolius* L., *Cistus albidus* L., *Clematis flamula* L., *Convolvulus althaeoides* L., *Cytisus scoparius* L., *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Marrubium incanum* Desr., *Silene vulgaris* (Moench) Garcke, *Trifolium campestre* Schreb., *T. scabrum* L. and *Veronica dillenii* Crantz. In addition, different plant parts were frequently collected and again rejected, such as parts of leaves, stems, petals and parts of infructescences like capsule walls and awns.

The composition of the seed and fruit intake largely corresponded with the successive plant species' flowering periods and the resulting seed production during the observation period. The most-collected plant species were recorded for each sampling season together with their flowering seasons (Table 1). In each sampling season, seeds and fruits of the most-collected plant species comprised more than 50% of the seed intake. Additionally, the distributional pattern of the main food resources changed constantly during the three sampling seasons.

Animal remains were found in greater quantities only in May 2009, when the production of fresh seeds and fruits was sparse (Fig. 2). The most animal material was collected in May 2009 (2.6% of the total amount of harvested material) versus between 0.6% and 0.7% in July-August 2009 and October 2009, respectively. The workers harvested a wide variety of animal remains, including dead arthropods, land dead snails, as well as dead marine gastropods. With the exception of living gastropods, which were picked from plant stems and the soil surface, *M. wasmanni* workers transported only dead arthropods to the nest. Workers were never observed to hunt.

The quantity of collected small stones and particles of soil was clearly the highest in July-August 2009.

Table 1. Main harvested food plants of *M. wasmanni* in the foraging area. Plant species are listed in in order of their flowering season and the resulting fruiting period, from May to October 2009. The percentage of seeds and fruits of each species in samples of the seed collection in May, July-August and October 2009 is shown. Shaded fields mark flowering months for each plant species. Respective months are labeled by roman numerals.

Plant family	Plant species	Fruit type	IV	V	VI	VII	VIII	IX	X
Fabaceae	<i>Securigera cretica</i> (L.)	Seeds, parts		9.61					
	Lassen	of pods							
Geraniaceae	<i>Erodium cicutarium</i> (L.)	Schizocarp		11.48					
	L'Hér. ex Aiton								
Poaceae	<i>Avena barbata</i> L.	Spikelets		19.09					
Poaceae	<i>Brachypodium distachyon</i> (L.) P. Beauv.	Spikelets		19.09					
Poaceae	<i>Aegilops ovata</i> L.	Spikelets				13.54			
Poaceae	<i>Aegilops triuncialis</i> L.	Spikelets				11.51			
Poaceae	<i>Avena barbata</i> L.	Spikelets				11.84			
Poaceae	<i>Brachypodium distachyon</i> (L.) P. Beauv.	Spikelets				17.94			
Poaceae	<i>Desmazeria rigida</i> L.	Spikelets				20.81			
Asparagaceae	<i>Asparagus acutifolius</i> L.	Berries						8.70	
Fabaceae	<i>Medicago minima</i> L.	Pods							17.31
Malvaceae	<i>Malva sylvestris</i> L.	Schizocarp							12.81
Poaceae	<i>Aegilops ovata</i> L.	Spikelets							14.15
Ranunculaceae	<i>Clematis flamula</i> L.	Seeds							9.57

Surface activity at the individual level

Morphology

Mean head widths of small-, media- and large-sized workers were found to be significantly different using a one-way analysis of variance ($R^2=0.91$, $F=8003$, $P<0.0001$). Three arbitrarily demarcated size categories of workers in mature colonies were distinguished by the head width: major- (head width: $2.62 \text{ mm} \pm 0.15 \text{ mm}$, mean \pm SD, $N = 500$), media- (head width: $1.75 \text{ mm} \pm 0.26 \text{ mm}$, mean \pm SD, $N = 500$) and minor-sized workers (head width: $1.11 \text{ mm} \pm 0.13 \text{ mm}$, mean \pm SD, $N = 500$).

Size matching

A linear regression analysis was performed for the ant head width and load ratio parameters ($R^2=0.14$ and $p=0.0001$). The results revealed a low negative correlation between ant head width and load ratio. Minor-sized workers showed a larger range within the load ratio than major-sized workers: the larger the worker size class, the smaller the range in the load ratio. The low positive correlation between ant head width and load size ($R^2=0.02$ and $p=0.0001$), in contrast, indicates that major-sized workers carry larger loads in comparison to minor-sized workers. Due to a wide variety of load types harvested and consumed by *M. wasmanni*, the results show that minor-sized workers more frequently collected smaller loads than major-sized workers. For example, larger loads such as spikelets of *Aegilops ovata* L. and *A. triuncialis* L. were collected more often by major- and media-sized workers and only occasionally by minor-sized workers. Otherwise, each worker size class frequently collected small loads such as fruits of *E. cicutarium* and *V. dillenii*. Fig. 3 shows ant head width versus load size, and Fig. 4 plots ant head width versus load ratio.

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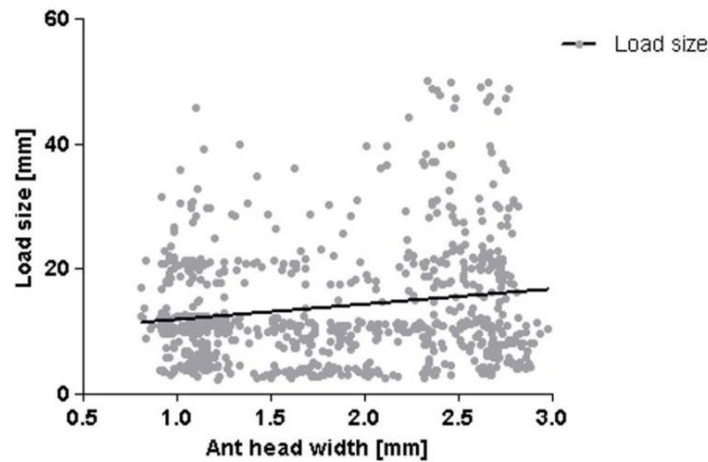


Figure 3. Scatter diagram load size versus ant size. Data are from random samples of returning foragers of a single *M. wasmanni* colony. One dot represents one observation ($N = 776$). Linear regression analysis revealed a very low positive correlation ($R^2 = 0.02$, $p = 0.0001$) between ant size and load size, indicating only a small tendency for major-sized workers to carry larger loads than minor-sized workers. Residuals from regressions were approximately normally distributed around zero in all cases.

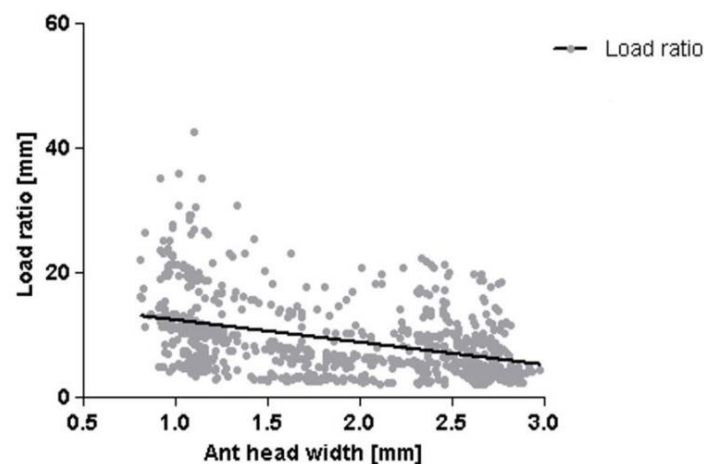


Figure 4. Scatter diagram load ratio versus ant size. The load ratio was calculated as follows: ant size (head width) + load size/ant size. Data are from random samples of returning foragers of a single *M. wasmanni* colony. One dot represents one observation ($N = 776$). Linear regression analysis revealed a low negative correlation ($R^2 = 0.14$, $p = 0.0001$) between ant size and load ratio. The larger the worker size class, the smaller the range in the load ratio. Residuals from regressions were approximately normally distributed around zero in all cases.

Harvesting efficiency

As a general rule, foraging efficiency (proportion of loaded ants per size class over the total number of incoming foragers per size class) increased as a function of the colony activity. Thus, the percentage of loaded ants was positively and significantly correlated to that of flows of incoming ants (Table 2). Foraging efficiency varied over the seasons and between the size classes (Fig. 5). While foraging efficiency exhibited by media- and major-sized workers decreased considerably from May to October 2009, minor-sized workers displayed the opposite tendency by increasing the foraging efficiency from $59.3\% \pm 6.3\%$ (mean \pm SD), $N = 268$ in May 2009 to $67.8\% \pm 12.5\%$ (mean \pm SD), $N = 163$ in October 2009.

Table 2. Correlation (Pearson) between the total number of returning minor-, media- and major-sized workers to the nest and the percentage of loaded workers. Calculations were performed separately per size class and per season from May to October 2009. R^2 explained between 24-74% of the variance in harvesting efficiency between size classes and seasons. R^2 explains the percentage of the variance shared between two variables. N - the number of samples taken. p indicates the statistical significance. If the p-value is low, then the correlation is statistically significant.

	Minor-sized workers	Media-sized workers	Major-sized workers
May	$R^2 = 0.240$ N = 34 p>0.0033	$R^2 = 0.398$ N = 34 p<0.0001	$R^2 = 0.469$ N = 34 p<0.0001
July-August	$R^2 = 0.58$ N = 34 p<0.0001	$R^2 = 0.55$ N = 34 p<0.0001	$R^2 = 0.710$ N = 34 p<0.0001
October	$R^2 = 0.743$ N = 34 p<0.0001	$R^2 = 0.633$ N = 34 p<0.0001	$R^2 = 0.480$ N = 34 p<0.0001

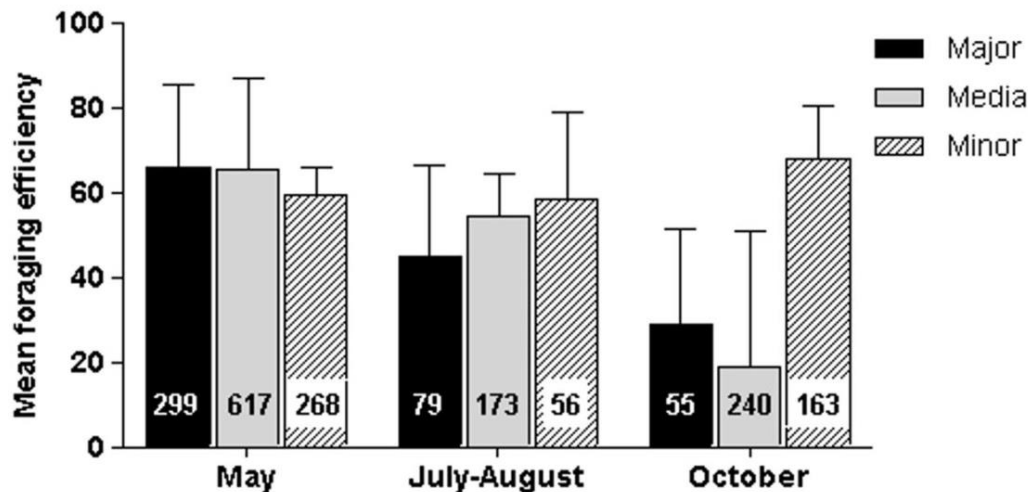


Figure 5. Mean foraging efficiency (in %) per day. Calculations were performed separately per size class and per season. Foraging efficiency varied considerably over the seasons and between size classes. Sample size represented by numbers in bars. Minor = minor-sized workers, Media = media-sized workers, Major = major-sized workers.

Speed related to soil surface temperature

Although workers of the ant species are highly variable in size, body size does not significantly influence the speed of burdened ($R = 0.027$, $p = 0.743$, $N = 153$) and unburdened ants ($R = 0.015$, $p = 0.859$, $N = 153$). Under natural conditions, the speed of a *M. wasmanni* worker either searching for food or returning to the nest with a load is significantly dependent upon soil surface temperature (Table 3). Nonetheless, the relationship between worker speed and soil surface temperature was very low for laden major-sized workers: soil surface temperature accounted for only 0.8% of the explained variance ($R^2 = 0.08$, $p < 0.001$). This value rises to 14.8% for unloaded major-sized workers ($R^2 = 0.148$, $p < 0.0001$). In both analyses, the dependent variable was worker speed and the independent variable was surface temperature.

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Table 3. Worker speed (cm/s) as a function of soil surface temperature (°C) analysed by a linear regression analysis. The dependent variable was worker speed, and the independent variable was soil surface temperature. R^2 value indicates how much of the total variation in the dependent variable can be explained by the independent variable. F-test has the null hypothesis that there is no linear relationship between the two variables (in other words $R^2 = 0$). Larger beta values are associated with the larger t-values and lower p-values. The t-statistics and the two-tailed p-values are used in testing whether a given coefficient is significantly different from zero. N - number of samples; df - degrees of freedom; p - the statistical significance of the regression model; B - values for the regression equation for predicting the dependent variable from the independent variable; Std. error - the standard errors associated with the coefficients; Beta - standardized coefficients; t - t-statistics; p - two-tailed p-values.

Variable	ANOVA					Unstandardized coefficients		Standardized coefficients		
	N	R ²	df	F	p	B	Std. error	Beta	t	p
Minor-sized unloaded	226	0.26	1	79.14	<0.0001	-0.27	0.03	-0.51	-8.90	<0.0001
Minor-sized loaded	275	0.23	1	82.70	<0.0001	-0.23	0.03	-0.48	-9.09	<0.0001
Media-sized unloaded	505	0.20	1	123.71	<0.001	-0.19	0.02	-0.44	-11.12	<0.0001
Media-sized loaded	476	0.32	1	218.52	<0.001	-0.32	0.02	-0.56	-14.78	<0.0001
Major-sized unloaded	208	0.15	1	35.83	<0.0001	-0.14	0.02	-0.39	-5.99	<0.0001
Major-sized loaded	146	0.08	1	12.53	<0.001	-0.13	0.04	-0.28	-3.54	<0.001

Discussion

The native food spectrum

Messor wasmanni is a harvester ant species that forms narrow trunk trails, typically dendritic in the form. These trunk trails reach total lengths up to 26.7 m and are used for foraging (Hölldobler & Wilson 1990). Near each ant nest, one to two trunk trails start as a single pathway that splits into branches and then into twigs. Workers clean these pathways from vegetation in order to allow large numbers of ants to travel easily (Hölldobler & Wilson 1990).

Under natural conditions, the diet of *M. wasmanni* is composed almost entirely of seeds, fruits and other plant materials such as green leaves and flower petals from a wide spectrum of plant species (Fig. 2). Granivory is a general trend of *Messor* species based on numerous observations for this genus (Hahn & Maschwitz 1985, Cerdá & Retana 1994, Detrain *et al.* 2000, Azcárate *et al.* 2005). The present study showed that *M. wasmanni* workers collect available food items not only from the soil surface (post-dispersal seed predation), but also directly from the mother plant (pre-dispersal seed predation), as was also reported by Hensen (2002). In addition, different plant parts were frequently collected and later rejected, presumably not serving as food; this included parts of leaves, stems, petals and infructescences such as capsule walls and awns. This observation agrees with the results by Hensen (2002) and Waser (1998) on the harvester ants *Messor bouvieri* Bondroit, 1918, *M. pergandei* (Mayr, 1886) and *M. timidus* Espadaler, 1997.

The distributional pattern of the main food resources changed constantly during the three sampling seasons. These observations allow the following conclusions: 1) main food plants occur in different regions of the foraging area; 2) some plant species grow in distinct small regions, while others are distributed over large areas of the foraging ground. Consequently, the foraging strategy of *M. wasmanni* workers is a mixture of individual foraging and column foraging, adjusted to the daily needs (Hölldobler & Wilson 1990). This foraging pattern is displayed by *Messor* spp. and *Pogonomyrmex* spp. (Hölldobler & Wilson 1990) and meets the following requirements: a) in order to discover newly-produced seed sources that are separated from each other, workers (patrollers) continuously explored the different parts of the foraging area; b) for the exploitation of seed sources that are concentrated in distinct small areas, ants exhibit a recruiting system by which large numbers of foragers are guided exactly to these rich accumulations of food items.

Concerning harvested animal remains, some authors (Brown *et al.* 1979, Baroni-Urbani 1987) have stated that granivorous ants prefer dead insects more than seeds. *Messor barbarus* (Linnaeus, 1767) workers can react with the intense recruitment and foraging activity to unusual protein food sources (Lopez *et al.* 1992). This behaviour was not been observed in the present study area: *M. wasmanni* workers only occasionally collected animal remains. Workers, however, harvested a variety of arthropod fragments, dead land snails, as well as dead marine gastropods. The most collected animal remains (2.6%) were found in May 2009, compared to 0.6% in July-August 2009 and 0.7% in October 2009. Animal remains probably represent a complementary protein source in the diet of *M. wasmanni*, confirming thus the interpretation by Azcárate *et al.* (2005). In addition, the sporadic collection of soil particles can be explained by the presence of resin exudates on them (Fernández-Escudero & Tinaut 1993).

Surface activity at the individual level

Morphology

Messor wasmanni workers show slight allometry with continuous size variation. These results agree with a preliminary investigation on the presence of allometric growth in *M. wasmanni* and *M. minor* (André, 1883) (Solida *et al.* 2007).

Size-matching

This study hypothesized that harvester ant species with a polymorphic worker caste such as *M. wasmanni* optimize food collection by delegating the task of carrying larger loads to larger workers and smaller loads to smaller workers (size-matching). Several evolutionary ecologists support the hypothesis that worker sizes or castes in social insects are distributed in an adaptive fashion (Brian & Jones 1980, Wilson 1980a, b, Porter & Tschinkel 1985, Hölldobler & Wilson 1990). Nonetheless, the evidence supporting this hypothesis is fairly sparse. Schmid-Hempel (1992) listed various published studies that deal with the “caste distribution function” – the frequency of different castes (physical, temporal) in a colony. These studies applied experiments and observations to test 1) corollaries of the hypothesis that the caste distribution function is adaptive, and 2) a more specific “ergonomic” hypothesis that adaptation involves efficiency of the colony in performing important tasks. A narrow majority of these studies provide support for the more general versions of the hypothesis, namely that social insect societies are efficiently organized in their physical or temporal caste structure. The remaining studies reviewed by Schmid-Hempel (1992), however, yielded apparent negative results. Moreover, evidence has accumulated that genetic, ontogenetic, seasonal and energetic factors can constrain size and caste ratios (e.g., Johnston & Wilson 1985, Rissing 1987, Schmid-Hempel 1992) and that behavioural flexibility of individual workers can weaken the link between these ratios and colony-level performance (Wilson 1983, Gordon 1996, Crosland *et al.* 1997).

The results presented here do not support the size matching hypothesis. Although there was a significant negative correlation between worker ant head width and load ratio and a positive correlation between worker head width and load size, the low to extremely low R^2 values explained only 2.8-14.9% of the variance in the size of loads. In addition, small-sized workers did not appear to be constrained by load size for the range of seeds available. There was only a slight tendency for minor-sized workers to carry smaller loads – in relation to their body size – than major-sized workers. In conclusion, the low to extremely low values of R^2 indicate that size-matching in *M. wasmanni*, while statistically significant, is biologically not significant.

Harvesting efficiency

Foraging activity of *M. wasmanni* on foraging trails is closely related to food availability (Detrain *et al.* 2000). Consequently, harvesting efficiency varied strongly from May to October. High numbers of foragers are often in close connection with an abundant food supply, as observed in *Novomessor albisetosus* (Mayr, 1886) and *N. cockerelli* (André, 1893) (Whitford *et al.* 1980), *Messor structor* (Latreille, 1798) (Hahn & Maschwitz 1985) and *Pogonomyrmex* spp. (Hölldobler 1976, Davidson 1977, Crist & MacMahon 1992).

This study showed that, on highly frequented, cleared foraging trails, *M. wasmanni* foragers brought not only greater quantities of food items to the nests, but also the proportion of laden ants over the total number of incoming foragers per size class increased as a function of the colony activity. Moreover, harvesting efficiency varied between size classes. While the harvesting efficiency of media- and major-sized workers decreased considerably from May to October 2009, the opposite tendency (increasing harvesting

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efficiency in the course of the year) was observed for minor-sized workers. Apparently, worker size is linked with numerous aspects of foraging, including load carriage potential, activity costs, trail-laying and risk susceptibility.

Worker castes are not equally endowed against predation or heat shock risks. The sensitivity to high temperatures is expected to decrease with worker size and cuticle thickness (Heredia & Detrain 2005). This may explain the high number of minor-sized workers present along foraging trails and the increased harvesting efficiency in October 2009. The decreasing harvesting efficiency of major-sized workers from May to October 2009 may reflect the specialization of this caste on the performance of other tasks such as cutting plant leaves, patrolling for favoured food sources (Gordon 2002), or defending functions as highlighted in *M. barbarus* (Detrain *et al.* 2000). *Messor wasmanni* major-sized workers are effective fighters against predators such as ant-eating zodariid spiders, which are very abundant in close proximity to ant nests and foraging trails in early summer and during summer (own unpublished observation).

Speed

Under natural conditions, the speed of loaded and unloaded *M. wasmanni* workers depends significantly on soil surface temperature. Nonetheless, the relationship of laden major-sized workers to soil surface temperature was minor – only 0.8% of the explained variance ($R^2 = 0.08$, $p < 0.001$). This value increases to 14.8% for unloaded major-sized workers ($R^2 = 0.148$, $p < 0.0001$). Similar relationships have been detected in *M. pergandei* (Rissing 1982), *M. capitatus* (Latreille, 1798) (Nielsen & Baroni-Urbani 1990), *Pogonomyrmex* spp. (Morehead & Feener 1998) and *M. barbarus* (Azcárate *et al.* 2007).

Conclusions

The results of this study show that, under natural conditions, *M. wasmanni* workers do not conduct size-matching at foraging trails. Little to none variance in the size of selected seeds and fruits can be attributed to forager body size. The minimal size-matching in *M. wasmanni* indicates that individual performance may be an inadequate measure of colony foraging success. Sources of variability such as worker size and the resulting difference in individual metabolism (Nielsen & Baroni-Urbani 1990) may play a more important role in the specific harvesting efficiency (Cerdá & Retana 1994). The sensitivity to high temperatures is expected to decrease with worker size and cuticle thickness, as also reported by Heredia & Detrain (2005). Moreover, the division of labour between workers of different size reflect a balance between the energetic gain for the colony, the need for cooperative food exploitation and the susceptibility to predation.

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6.2. *Manuscript I*

Analyse des Abfallmaterials der mediterranen Ernteameise *Messor wasmanni* Krausse, 1910 (Hymenoptera: Formicidae) – Teil 1 botanischer Anteil



Foto by T. Traxler

Analyse des Abfallmaterials der mediterranen Ernteameise *Messor wasmanni* Krausse, 1910 (Hymenoptera: Formicidae) Teil 1: botanischer Anteil

T. TRAXLER

A b s t r a c t: *Messor wasmanni* Krausse, 1910 (Formicidae, Myrmicinae) is a harvester ant occurring in the southeastern Mediterranean region including the North Dalmatian island of Cres, where it settles in the central and southern area which is characterized by Mediterranean climate. Within the local distribution area at the island, near Merag and Loznati in the north, in the middle area between Martiščica/Zaglav and Belej and in the southern part of the island near Osor and Punta Križa, comprehensive investigations on the ants' biology, especially a qualitative and quantitative analysis of collected food items was performed in the years 2009/10. As with all *Messor* species, the diet of *M. wasmanni*, is chiefly composed of seeds (granivory) (90,9 %), but they consume to a minimum extent animal remains (arthropods and snails) as well. Plant parts, not serving as food are rejected and accumulate to chaff piles at the nest surfaces. These chaff piles were subject of a close analysis. They comprised 55 plant species belonging to 20 families. Furthermore, 21 types of dispersal units (diaspores) and plant parts were identified. Germinable seeds made up 7.5%, indicating that harvester ants may play an important role in the dynamics of plant communities by both acting as seed dispersal agents and as seed predators. The remaining 9.1% consisted of animal remains and faeces of orthoptera Olivier, 1789. 43 animal taxa were identified. Gastropoda dominated with a relative frequency of 53%, followed by Coleoptera (38%). Animal remains may represent a complementary protein source in the diet, especially when seeds and fruits are scarce in spring and during periods of drought.

Z u s a m m e n f a s s u n g: *Messor wasmanni* Krausse, 1910 (Formicidae, Myrmicinae) ist eine Ernteameise des südöstlichen Mediterrangebietes und besiedelt auch die norddalmatinische Insel Cres in Kroatien. Hier ist ihr Vorkommen auf den zentralen und südlichen Inselbereich mit mediterranem Klimaeinfluss begrenzt. Innerhalb dieses lokalen Verbreitungsgebietes von Merag und Loznati im Norden, dem mittleren Bereich zwischen Martiščica/Zaglav und Belej sowie dem Süden der Insel bei Osor und Punta Križa erfolgten 2009/10 umfangreiche Untersuchungen zur Biologie, insbesondere zum qualitativen und quantitativen Nahrungseintrag. Wie alle *Messor*-Arten, ernährt sich *M. wasmanni* überwiegend granivor von Pflanzensamen (90,9 %), konsumiert gelegentlich aber auch Insekten und sogar Schnecken. Nicht mehr benötigte oder verwertbare Pflanzenreste und Samen werden als Abfallhaufen in Nestnähe abgelegt und ermöglichen somit deren nähere Analyse. Insgesamt konnten 55 Pflanzenarten aus 20 Familien, 21 Typen pflanzlicher Diasporen und andere Pflanzenteile identifiziert werden. Samen waren mit einem Anteil von 7.5% vertreten. Dieser relativ hohe Anteil an noch intakten und keimfähigen Samen im Abfallmaterial deutet darauf hin, dass Ernteameisen, trotz ihrer granivoren Ernährungsweise, eine bedeutende Funktion in der Weiterverbreitung von verschiedenen Pflanzenarten einnehmen. Der restliche Anteil von 9.1% setzte sich aus tierischen Überresten und Faeces von Orthoptera Olivier, 1789 zusammen. 43 tierische Taxa wurden identifiziert. Gastropoda überwiegen mit 53% Häufigkeit. 38% des tierischen Abfallmaterials entfallen auf die Coleoptera. Es wird angenommen, dass der gelegentliche Verzehr von Insekten und Schnecken eine zusätzliche Proteinquelle darstellt, vor allem, wenn pflanzliche Nahrung im Frühjahr noch rar ist oder durch sommerliche Dürreperioden stark reduziert wird.

Key words: Ernteameisen, *Messor*, Abfallmaterial, Diasporen, Samen,

Granivorie.

Einleitung

Als Ernteameisen werden Arten zusammengefasst, deren Nahrung sich vornehmlich aus Samen verschiedener Pflanzenarten zusammensetzt. Dieser Ernährungstyp wird als Granivorie bezeichnet (BACH 2013). Die Gattung *Messor* Forel, 1890 umfasst etwa 40 Arten, welche, abgesehen von wenigen Ausnahmen (HAHN & MASCHWITZ 1985), vor allem in trockenen Gebieten im mediterranen Raum Südeuropas, Afrikas und Asiens (HÖLLDOBLER & WILSON 1990) vorkommen. Nahrung wird in der weiteren Umgebung des Nests gesammelt, eingetragen und in Kammern bis zur weiteren Verarbeitung zu Ameisenbrot gelagert. Um das Auskeimen bzw. die Zersetzung der Samen durch Pilze und Bakterien zu verhindern, wird von den Arbeiterinnen metapleurales Drüsensekret auf diese aufgetragen. (SCHILDKNECHT & KOOB 1971, CELLI & MACCAGNANI 1994). Auf diese Weise können Ernteameisen Dürre- oder Frostperioden überleben (HÖLLDOBLER & WILSON 1990). Nicht verwertbare Pflanzenteile werden aus dem Nest ausgetragen und akkumulieren direkt auf der Nestoberfläche regelrecht zu durchaus größeren Abfallhaufen. Dieses Abfallmaterial repräsentiert das Nahrungsspektrum der Kolonie sowohl in der Artzusammensetzung der Nahrungspflanzen als auch in der relativen Häufigkeit von Samen der einzelnen Arten (STEINBERGER ET AL. 1991).

In dieser Studie wurde zum einen die Nestoberfläche mehrerer *Messor wasmanni* Kolonien analysiert und zum anderen das Spektrum an Pflanzenarten im Abfallmaterial untersucht.

Material und Methoden

Klima, Vegetation und Untersuchungsflächen

Der Norden und Nordosten der Insel Cres, SSW der Halbinsel Istrien, wird durch kühleres, feuchtes submediterranes Klima charakterisiert. Im Westen und Süden herrscht hingegen mediterranes Klima mit trockenen, meist heißen Sommermonaten und mildem bis kühlem und niederschlagsreichem Winter. *M. wasmanni* kommen nur in der mediterranen Klimazone der Insel Cres vor und meidet die meist geschlossenen Laubwälder im Norden der Insel.

Der Vegetationstyp auf den Untersuchungsflächen von Merag/Loznati (I), ist eine mediterrane Strauchheiden-Formation mit fuß- bis kniehohen, selten über 1 m hohen Kleinsträuchern, Geophyten, Therophyten, Rosetten- und Horstpflanzen und wird hier vereinfachend als „Garigue“ definiert. Die Flächen bei Martinsčica/Zaglav (IIa), Belej (IIb) und Punta Kriča (IIIa) entsprechen unterschiedlichen Trockenrasen-Gesellschaften und jene bei Osor (IIIb) an Süden der Insel ist Teil einer verlandeten mittelalterlichen Saline in unmittelbarer Meeresnähe, z. T. mit halophilem Charakter (Abb. 1).

Untersuchungsflächen I: im Norden des Verbreitungsgebietes der Ernteameise *M. wasmanni* auf der Insel Cres:

- Merag: Seehöhe: 138.4 m, 44° 57' N, 14° 27' E
- Loznati: Seehöhe: 249.4 m, 44° 55' N, 14° 26' E

Die untersuchten Ameisenkolonien lagen in Merag entlang eines Feldweges bzw. am Rande einer Schafweide in Loznati.

Die pflanzengeographisch charakteristische Karsttriften- und Weidelandschaft auf Merag

und Loznati sind von der Bora beeinflusste steinige *Stipo- Salvietum officinalis*- und *Festuco-Koelerietum splendentis* – Gesellschaften, einerseits mit starker Einnischung von *Juniperus oxycedrus* L., *Paliurus spina-christi* Mill. und *Rhamnus intermedius* Steud. & Hochst., andererseits mit Übergängen zu Gariguen ähnlichen Gesellschaften (GAZI-BASKOVA 1975).

Die *Stipo-salvietum officinalis*-Vergesellschaftung ist entlang der Adriatischen Küste weit verbreitet und stellt eine der häufigsten Pflanzengesellschaften im mediterranen Raum dar. Charakterpflanzen sind *Salvia officinalis* L. und *Stipa bromoides* (L.). Häufige Pflanzen sind *Bromus erectus* Huds., *Helichrysum italicum* (Roth) G. Don, *Brachypodium retusum* (Pers.) P. Beauv. 1812, *Aethionema saxatile* (L.) W. T. Aiton, *Teucrium montanum* L., *Asparagus acutifolius* L., und *Dactylis glomerata* L. subsp. *hispanica* (Roth) Nyman (STANČIĆ & PANDŽA 2005).

Auf Weideflächen in Loznati sind nitrophile Arten der *Scolymo-marrubietum incanae* - Gesellschaft häufig vertreten (GAZI-BASKOVA 1975).

Untersuchungsflächen II a,b: in der Mitte des Verbreitungsgebietes:

- Zaglav: Seehöhe: 6.5 m, 44° 48' N, 14° 21' E
- Belej: Seehöhe: 132.4 m, 44° 46' N, 14° 25' E

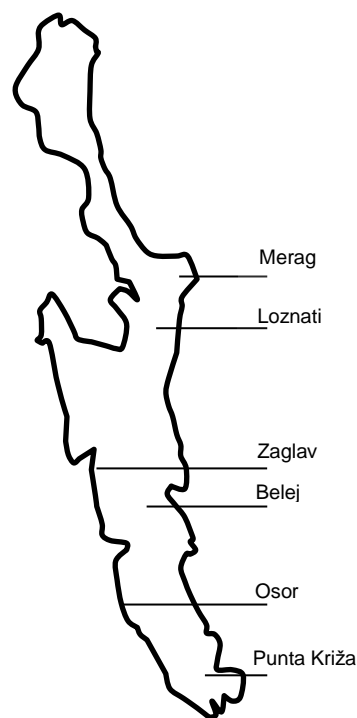


Abb. 1: Landkarte der Insel Cres. Eingezeichnet sind die Flächen, an denen Abfallmaterial eingesammelt wurde. Sie befanden sich im nördlichen (N), im mittleren (M) sowie im südlichen Bereich (S) des Verbreitungsgebietes von *M. wasmanni* auf der Insel Cres. — Fig. 1: Geographical map of the island of Cres. The study areas in the northern distribution zone (N), in the middle (M) and in the southern distribution zone (S) of the harvester ant *M. wasmanni* at the island are marked.

Auch die Fläche bei Zaglav wird durch eine *Stipo-salvietum officinalis* - Gesellschaften charakterisiert. Ameisenkolonien befanden entlang eines Feldweges in Meeresnähe. In Belej wurden Ameisenkolonien auf einer ungenutzten Schafweide ausgewählt. Die ausgedehnten Trockenrasen bei Belej gehören verschiedenen Vegetationsverbänden an, welche unter anderem besonders reich an Asteraceen, Fabaceen sowie an *Brachypodium Chrysopogenetia* – Gesellschaften und *Cymbogonion ramosi* - Gesellschaften sind (GAZI-BASKOVA 1975). *Festuco-koelerietum splendentis* - Gesellschaften treten hier in Arealen mit relativ wenig menschlichem Einfluss auf (STANČIĆ & PANDŽA 2005).

Untersuchungsflächen III a,b: im Süden des Verbreitungsgebietes:

- Punta Križa: Seehöhe: 40.0 m, 44° 41' N, 14° 23' E
- Osor: Seehöhe: 0.0 m, 44° 39' N, 14° 28' E

Die Ameisenkolonien in Punta Križa befanden sich auf einer Schafweide, charakterisiert durch nitrophile *Scolymo-marrubietum incane* - Gesellschaften, jene bei Osor befanden sich auf Salzwiesen in unmittelbarer Meeresnähe. Azonale Mediterrane Salzmarschen von Osor werden dominiert von Salzbinsen-Gesellschaften *Juncetia maritime* – Gesellschaften mit Beständen der

Meeresstrandbinse, Gliedermelden-Gesellschaften, *Arthrocnemetea* – Gesellschaften sowie in unmittelbarer Ufernähe und auf höher gelegenen, stärker ausgesüßten Flächen von Kleinbinsenrasen und *Nanojuncetea-marrubietum incanae* - Gesellschaften (MARTINOLI 1948).

Mikroklima

Das Mikroklima wurde an den Standorten I-III mittels 6 beschatteten, auf der Bodenoberfläche ausgelegten Dataloggern (PCE-HT71) während des gesamten Untersuchungszeitraumes erhoben. Der Messzeitraum erstreckte sich vom 28. 05. 2009 bis 24. 10. 2009. Beide Datalogger aus Osor und Punta Križa wurden beschädigt aufgefunden, weshalb hier keine Daten existieren.

Beschreibung und Vermessung von *M. wasmanni* Nestoberflächen

M. wasmanni Kolonien legen tiefe Erdnester an, an deren Oberfläche nicht verwertbare Nahrungsüberreste (Abfallmaterial) zu flachen Erhebungen akkumulieren. Der größte Durchmesser der vegetationsfreien, rundlichen Nestoberflächen, sowie die Distanz zwischen Nesteingang und Abfallmaterial wurden von 35 Nestern erhoben.

Abfallmaterial

Ende Oktober 2009 wurde der organische Abfall der einzelnen untersuchten Kolonien (hier als „Abfallmaterial“ bezeichnet), welcher von den Ameisen während der aktiven Saison vom Ende der Winterruhe im Frühjahr bis zum Herbst in Nestnähe abgelagert worden war, für die spätere Bestimmung des Inhaltes eingesammelt. Für jede Kolonie wurde das Gewicht des Abfallmaterials mit einer Waage (Mettler MP 4600) ermittelt. Um die vermutbare Fauna der gesammelten Proben bis zu ihrer Konservierung nicht zu schädigen, konnte statt des Trockengewichtes nur das Frischgewicht ermittelt werden. Zur qualitativen und quantitativen Analyse des Pflanzenspektrums im Abfallmaterial der Untersuchungsflächen I-III wurden von jeweils zehn Kolonien 100g entnommen. Das ergibt eine Gesamtmenge von insgesamt drei Kilogramm. Enthaltene Diasporen, Pflanzenfragmente, wurden möglichst auf Art- bzw. Gattungsniveau bestimmt. Der umfangreiche faunistische Inhalt an tierischen Überresten und lebenden Arthropoden ist Thema einer eigenen Publikation (WAITZBAUER, TRAXLER, ČURČIĆ 2017, in Vorbereitung).

Auswertung

Der durchschnittliche Durchmesser (mean \pm SD) von *M. wasmanni* Nestoberflächen, die durchschnittliche Distanz (mean \pm SD) zwischen Nesteingang und Abfallmaterial (N = 35), sowie das durchschnittliche Frischgewicht (mean \pm SD) des Abfallmaterials aus Standort I-III wurde errechnet (N = 30).

Aus den Rohdaten wurde die relative Häufigkeit der Pflanzenarten berechnet und nach Dominanzklassen nach ENGELMANN (1978) eingeteilt. Für im Abfallmaterial vorkommende Diasporen und Pflanzenteile wurde deren Prozentanteil an der Gesamtmenge errechnet.

Die Diversität des Abfallmaterials aus den jeweiligen Standorten wurde über die Berechnung des Diversitätsindex nach Shannon-Weaver (H'), die maximale Diversität (H_{max}) und der Evenness (E) erfasst. Mögliche Unterschiede der Artzusammensetzung des Abfallmaterials konnten mit dem Jaccard Index ausgedrückt werden.

Ergebnisse

Mikroklima

Vom Frühjahr bis Herbst 2009 durchgeführte Temperatur-Messungen ergaben aufgrund der räumlichen Distanz der Untersuchungsflächen I-II einen auffälligen Temperaturunterschied. Im Durchschnitt ist es in Meeresnähe (Zaglav) sowie auf offener, windexponierter Fläche (Belej) um 4.8 °C kühler als auf einem sonnenexponierten Hang der Halbinsel Merag (Abb. 2).

Auffallend ist auch die Differenz zwischen den gemessenen Luftfeuchtigkeitswerten an beiden Untersuchungsflächen. Sie liegen auf Fläche I während der gesamten Messperiode um durchschnittlich 8.5% rel. LF unter jenen von Fläche II (Abb. 3).

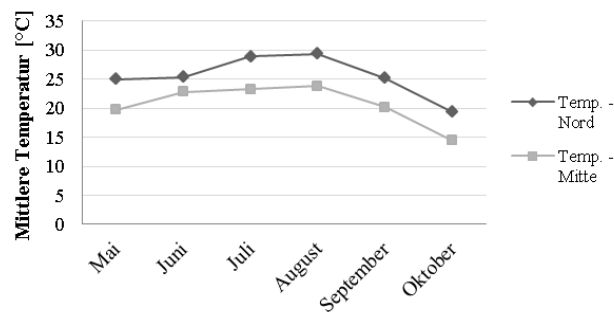


Abb. 2: Monatsmittel der Temperatur vom 28. Mai bis 24. Oktober 2009 für Norden (Merag, Loznati) und der Mitte (Zaglav, Belej) des Verbreitungsgebietes von *M. wasmanni* auf der Insel Cres. — Fig. 2: Mean temperature in the north (Merag, Loznati) and middle (Zaglav, Belej) of the distribution zone of *M. wasmanni* at the island of Cres from 28. May to 24. October 2009.

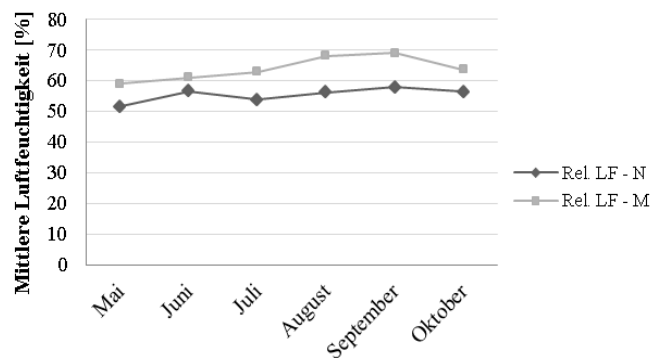


Abb. 3: Monatsmittel der relativen Luftfeuchtigkeit vom 28. Mai bis 24. Oktober 2009 für Norden (Merag, Loznati) und der Mitte (Zaglav, Belej) des Verbreitungsgebietes von *M. wasmanni* auf der Insel Cres. — Fig. 3: Mean relative humidity in the north (Merag, Loznati) and middle (Zaglav, Belej) of the distribution zone of *M. wasmanni* at the island of Cres from 28. May to 24. October 2009.

Analyse des Abfallmaterials

Frischgewichtes Abfallmaterials

Tab. 1: Vergleich des Frischgewichtes des Abfallmaterials aus Standort I-III. — Tab. 1: Comparison of the fresh weight of chaff pile material collected on site I-III.

Standort	N	Minimum (g)	Maximum (g)	Mean (g)	Std. Abw.
I	11	405.0	1120.0	771.5	234.8
II	10	475.0	1284.0	802.2	256.5
III	11	529.0	1987.0	1008.0	461.3

Das Frischgewicht des Abfallmaterials variierte beträchtlich von 771.5 g im Norden zu 1008.0 g im Süden (Tab. 1).

Prozentuelle Zusammensetzung des Abfallmaterials:

Das von Arbeiterinnen ins Nest eingetragene Material wurde in drei Kategorien gegliedert: 1) Diasporen; 2) Pflanzenteile wie Blätter, Stängel sowie Blütenblätter; 3) Arthropodenreste und Orthoptera-faeces sowie Gastropoda.

Insgesamt umfasste der Gesamtanteil von pflanzlichem Material im Abfallmaterial 90.9%. Der restliche Anteil von 9.1% setzte sich aus tierischen Überresten und Faeces zusammen. Es wurde eine Gesamtanzahl 55 Pflanzenarten aus 20 Familien (Tab. 2) sowie zahlreichen tierische Taxa identifiziert. Gastropoda dominierten mit 53% relativer Häufigkeit im tierischen Material, welche sich auf 26 Taxa (auf Art- und Gattungsniveau) verteilten. Mit 38% relativer Häufigkeit repräsentierten Coleoptera die zweithäufigste Tiergruppe (siehe dazu WAITZBAUER, TRAXLER, ČURČIĆ 2017 in Vorber.).

Vergleicht man die Zusammensetzung des Abfallmaterials der drei Untersuchungsflächen, erkennt man deutliche Unterschiede im Anteil des darin vorkommenden pflanzlichen und tierischen Materials (Abb. 4). Der höchste pflanzliche Anteil war im Abfallmaterial von Fläche I zu finden. Es setzte sich aus 99.5% pflanzlichem Material und 0.5% tierischer Überreste zusammen. Dem gegenüber, wurde im Abfallmaterial aus Standort II der größte Anteil an tierischem Material (16.9%) nachgewiesen, pflanzliches Material machte hier 83.1% aus.

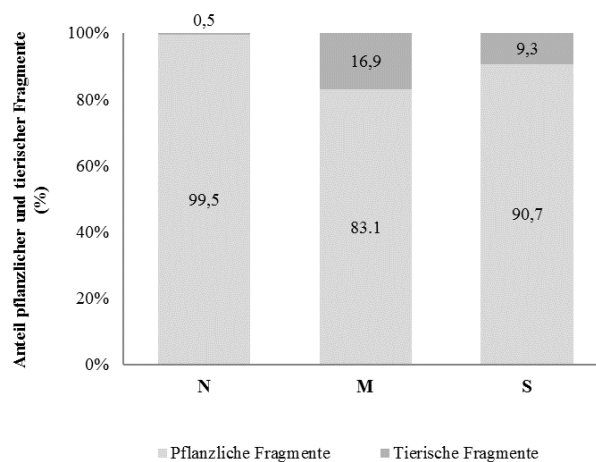


Abb. 4: Prozentanteil an pflanzlichem und tierischem Material im Abfallmaterial. Norden (Merag, Loznati) = Standort I, Mitte (Zaglav, Belej) = Standort II, und Süden (Osor, Punta Križa) = Standort III des Verbreitungsgebietes von *M. wasmanni* Kolonien. — Fig. 4: Percentage share of plant material and animal remains in chaff piles of *M. wasmanni*. Samples were taken in the north (Merag, Loznati) = site I, middle (Zaglav, Belej) = site III and south (Osor, Punta Križa) = site III.

Dominanzverhältnisse der Pflanzenarten im Abfallmaterial:

Insgesamt wurden 55 Pflanzenarten nachgewiesen. Tabelle 2 gibt die Zuordnung der Arten in Dominanzklassen nach ENGELMANN (1978) wieder. Insgesamt wurden zwei eudominante und vier dominante Arten festgestellt.

Auf Fläche I kamen 42 Arten vor, welche sich auf 18 Familien verteilten. Als einzige eudominante Art war *Erodium cicutarium* L. (Geraniaceae) mit 47.9% relativer Häufigkeit vertreten. Die Familie der Geraniaceae wurde ausschließlich im Abfallmaterial aus dem Norden verzeichnet.

Subdominant vertreten waren *Tordylium apulum* L. (Apiaceae), *Urospermum picroides* L. (Cichoriaceae), *Medicago minima* L. (Fabaceae), *Trifolium scabrum* L. (Fabaceae) und *Avena sterilis* L. (Poaceae).

Die Familie der Poaceae waren am häufigsten vertreten durch *Aegilops ovata* L. und *Avena sterilis* L. Beide Arten kamen im Norden zahlenmäßig am häufigsten vor, jedoch waren sie auch auf Standort II und III vertreten.

Funde von *Daucus carota* L. (Apiaceae), *Scolymus hispanicus* L. (Asteraceae), *Capsella rubella* Reut. (Brassicaceae), *Petrorhagia saxifraga* L. (Caryophyllaceae), *Anthyllis vulneraria* L. (Fabaceae), *Astragalus hamosus* L. (Fabaceae), *Trifolium stellatum* L. (Fabaceae), *Marrubium vulgare* L. (Lamiaceae), *Salvia officinalis* L. (Lamiaceae), *Linum austriacum* L. (Linaceae), *Malva sylvestris* L. (Malvaceae), *Aegilops triuncialis* L. (Poaceae), *Anthoxanthum odoratum* L. (Poaceae), *Catapodium rigidum* Hubb. (Poaceae), *Hordeum murinum* L. (Poaceae), *Stipa* sp. (Poaceae), *Vulpia ciliata* Dumort. (Poaceae) sowie *Rumex obtusifolius* L. (Polygonaceae) wurden nur an diesem Standort nachgewiesen.

Auf Fläche II war die Diversität mit 43 Arten aus 11 Familien am größten. Die einzige eudominante Art war *Medicago minima* L. mit 58.1% relativer Häufigkeit. Charakteristisch war das Vorkommen von *Convolvulus althaeoides* L. (Convolvulaceae) mit 22.5% Dominanzanteil. Lediglich einzelne Funde dieser Art kamen im Abfallmaterial aus dem Norden vor.

Subdominante Arten waren *Aegilops neglecta* Req. (Poaceae) sowie *Echium plantagineum* L. (Plantaginaceae), wobei von letzterer Art nur Einzelfunde im Norden nachgewiesen

wurden, im Süden war sie nicht vertreten.

Crepis dioscoridis L. (Asteraceae) wurde als Einzelfund verzeichnet.

Fläche III zeichnete sich floristisch mit 26 Pflanzenarten aus 12 Familien als artenärmste Fläche aus.

Dominante Arten waren *Zacintha verrucosa* Gaertn., *Trifolium campestre* Schreb. (Fabaceae) und *Trifolium scabrum* L. (Fabaceae). *Zacintha verrucosa* Gaertn. war im Abfallmaterial aus allen Standorten zu finden, quantitativ jedoch am häufigsten im Süden vertreten.

Subdominante Arten waren *Carthamus lanatus* L. (Asteraceae), *Scorpiurus muricatus* L. (Fabaceae), *Trigonella balansae* Boiss & Reut (Fabaceae), *Plantago lanceolata* L. (Plantaginaceae) und *Dasyphyrum villosum* (L.) Borbás (Poaceae).

Diversität in der Familie der Poaceae war auf Fläche III am geringsten: *Aegilops ovata* L. machte den Hauptanteil aus, vereinzelt traten *Avena sterilis* L., *Cynosurus echinatus* L. sowie *Melica ciliata* L. auf.

Der Fund von *Carduus pycnocephalus* L. (Asteraceae) und *Trigonella corniculata* L. (Fabaceae) sowie das häufige Vorkommen von *Anthoxanthum odoratum* L. (Poaceae) und *Cynodon dactylon* Pers. (Poaceae) stellen eine Besonderheit für das Abfallmaterial aus dem Süden dar.

Tab. 2: Wiederfindungsrate in Prozent von der Gesamtanzahl der im Abfallmaterial nachgewiesenen Nahrungspflanzen. Hellgrau: eudominante, dominante und subdominante Arten. Dunkelgrau: Pflanzenarten, welche auf allen drei Untersuchungsflächen im Abfallmaterial auftraten. — Tab. 2: Recovery rate in percent of food plants occurred in chaff piles. Light grey: eudominant and dominant plant species, dark grey: plant species that occurred in chaff piles in each of the three sampling sites.

Familie	Art	Verbreitungseinheit	Untersuchungsfläche I		Untersuchungsfläche II		Untersuchungsfläche III	
			%	Dominanz- klasse	%	Dominanz- klasse	%	Dominanz- klasse
Apiaceae	<i>Daucus carota</i> L.	Spaltfrucht	0.35	subrezent	0.00	-	0.00	-
Apiaceae	<i>Foeniculum vulgare</i> Mill.	Spaltfrucht	0.00	-	0.23	sporadisch	0.00	-
Apiaceae	<i>Tordylium apulum</i> L.	Spaltfrucht	4.45	subdominant	0.00	-	0.06	sporadisch
Asteraceae	<i>Carduus pycnocephalus</i> L.	Achäne	0.00	-	0.00	-	0.38	subrezent
Asteraceae	<i>Carthamus lanatus</i> L.	Achäne	1.31	rezedent	2.06	rezedent	5.22	subdominant
Asteraceae	<i>Crepis dioscoridis</i> L.	Blütenkopf	0.47	subrezent	0.01	sporadisch	0.00	-
Asteraceae	<i>Scolymus hispanicus</i> L.	Achäne	1.38	rezedent	0.00	-	0.00	-
Asteraceae	<i>Crepis verrucosa</i> Gaertn.	Teilfrucht	0.00	-	0.00	-	14.49	dominant
Asteraceae	<i>Crepis verrucosa</i> Gaertn.	Blütenkopf	0.71	subrezent	0.00	-	0.26	sporadisch
Boraginaceae	<i>Echium plantagineum</i> L.	Nüßchen	0.11	sporadisch	7.30	subdominant	0.00	-
Brassicaceae	<i>Capsella rubella</i> Reut.	Hülsenhälfen	0.74	subrezent	0.00	-	0.00	-
Caryophyllaceae	<i>Petrohragia saxifraga</i> L.	Kapselfrucht	0.59	subrezent	0.00	-	0.00	-
Caryophyllaceae	<i>Silene vulgaris</i> Gareke	Kapselfrucht	0.00	-	0.01	sporadisch	0.00	-
Cichoriaceae	<i>Urospermum picroides</i> L.	Achäne	3.31	subdominant	0.00	-	0.02	sporadisch
Cistaceae	<i>Helianthemum</i> sp.	Kapselfrucht	0.04	sporadisch	0.00	-	0.86	subrezent
Convolvulaceae	<i>Convolvulus althaeoides</i> L.	Samen	0.88	subrezent	22.51	dominant	0.00	-
Euphorbiaceae	<i>Euphorbia wulfenii</i> Hoppe	Samen	0.30	sporadisch	0.06	sporadisch	0.05	sporadisch
Fabaceae	<i>Anthyllis vulneraria</i> L.	Hülse	1.10	rezedent	0.00	-	0.00	-

Fabaceae	<i>Anthyllis vulneraria</i> L.	Kelch	1.01	rezedent	0.00	-	0.00	-
Fabaceae	<i>Astragalus hamosus</i> L.	Hülse	0.12	sporadisch	0.00	-	0.00	-
Fabaceae	<i>Lotus corniculatus</i> L.	Hülse	0.01	sporadisch	0.00	-	1.25	rezedent
Fabaceae	<i>Medicago arabica</i> L.	Hülse	0.93	subrezedent	0.00	-	0.44	subrezedent
Fabaceae	<i>Medicago carstiensis</i> L.	Hülse	0.00	-	0.07	sporadisch	0.07	sporadisch
Fabaceae	<i>Medicago rigidula</i> (L.) All.	Hülse	0.27	sporadisch	0.05	sporadisch	0.00	-
Fabaceae	<i>Medicago minima</i> L.	Hülse	6.55	subdominant	58.09	eudominant	2.24	rezedent
Fabaceae	<i>Medicago orbicularis</i> L.	Hülse	0.03	sporadisch	0.02	sporadisch	0.00	-
Fabaceae	<i>Scorpiurus muricatus</i> L.	Teilfrucht	0.00	-	0.18	sporadisch	7.35	subdominant
Fabaceae	<i>Trifolium campestre</i> Schreb.	Petale	0.50	subrezedent	0.00	-	30.88	dominant
Fabaceae	<i>Trifolium scabrum</i> L.	Kelch	5.61	subdominant	1.44	rezedent	11.11	dominant
Fabaceae	<i>Trifolium angustifolium</i> L.	Kelch	0.64	subrezedent	1.34	rezedent	0.00	-
Fabaceae	<i>Trifolium stellatum</i> L.	Kelch	0.17	sporadisch	0.00	-	0.00	-
Fabaceae	<i>Trigonella balansae</i> Boiss & Reut	Hülse	2.54	rezedent	0.00	-	3.84	subdominant
Fabaceae	<i>Trigonella balansae</i> Boiss & Reut	Blüte+Kelch	0.00	-	0.00	-	0.35	subrezedent
Geraniaceae	<i>Erodium cicutarium</i> L.	Teilfrucht	47.85	eudominant	0.00	-	0.00	-
Geraniaceae	<i>Erodium cicutarium</i> L.	Fruchtschnabel	3.61	subdominant	0.00	-	0.00	-
Lamiaceae	<i>Marrubium vulgare</i> L.	Kelch	0.96	subrezedent	0.00	-	0.00	-
Lamiaceae	<i>Marrubium vulgare</i> L.	Blätter	0.22	sporadisch	0.00	-	0.00	-
Lamiaceae	<i>Salvia officinalis</i> L.	Teilfrucht (Klausen)	0.51	subrezedent	0.00	-	0.00	-
Lamiaceae	<i>Salvia verbenacea</i> L.	Kelch	0.00	-	0.00	-	0.20	sporadisch
Lamiaceae	<i>Thymus vulgaris</i> L.	Kelch	0.00	-	0.00	-	0.59	subrezedent
Linaceae	<i>Linum austriacum</i> L.	Kapselfrucht	0.00	-	0.00	-	0.07	sporadisch
Linaceae	<i>Linum austriacum</i> L.	Kelch	0.62	subrezedent	0.00	-	0.00	-

Malvaceae	<i>Malva sylvestris</i> L.	Spaltfrucht	0.01	sporadisch	0.00	-	0.00	-
Plantaginaceae	<i>Plantago lanceolata</i> L.	Kapselfrucht	0.00	-	0.42	subrezent	5.53	subdominant
Plantaginaceae	<i>Plantago lanceolata</i> L.	Ähre	0.00	-	0.18	sporadisch	1.15	rezedent
Poaceae	<i>Aegilops neglecta</i> Req.	Ährchen	3.06	rezedent	5.32	subdominant	1.16	rezedent
Poaceae	<i>Aegilops triuncialis</i> L.	Ährchen	0.17	sporadisch	0.00	-	0.00	-
Poaceae	<i>Anthoxanthum odoratum</i> L.	Ährchen	0.00	-	0.00	-	1.64	rezedent
Poaceae	<i>Anthoxanthum odoratum</i> L.	Spelzen	0.00	-	0.00	-	0.95	subrezent
Poaceae	<i>Avena sterilis</i> L.	Ährchen	3.19	subdominant	0.14	sporadisch	0.37	subrezent
Poaceae	<i>Avena sterilis</i> L.	Grannen	0.04	sporadisch	0.00	-	0.00	-
Poaceae	<i>Anisantha sterilis</i> L.	Spelzen	0.60	subrezent	0.00	-	0.00	-
Poaceae	<i>Cynodon dactylon</i> Pers.	Ähre (Teile)	0.00	-	0.00	-	0.75	subrezent
Poaceae	<i>Cynosurus echinatus</i> L.	Ährchen	0.70	subrezent	0.26	sporadisch	0.00	-
Poaceae	<i>Dasyphyrum villosum</i> (L.) Borbás	Ährchen	0.00	-	0.00	-	5.99	subdominant
Poaceae	<i>Catapodium rigidum</i> Hubb.	Stängel	0.20	sporadisch	0.00	-	0.00	-
Poaceae	<i>Hordeum murinum</i> L.	Spelzen	1.14	rezedent	0.00	-	0.00	-
Poaceae	<i>Melica ciliata</i> L.	Ährchen	0.32	subrezent	0.21	sporadisch	0.00	-
Poaceae	<i>Poaceae</i> sp.	Spelzen	1.97	rezedent	0.00	-	0.00	-
Poaceae	<i>Stipa</i> sp.	Grannen	0.01	sporadisch	0.00	-	0.00	-
Poaceae	<i>Vulpia ciliata</i> Dumort.	Ährchen	0.34	subrezent	0.00	-	0.00	-
Polygonaceae	<i>Rumex obtusifolius</i> L.	Frucht + Valven	0.15	sporadisch	0.00	-	0.00	-
Primulaceae	<i>Anagallis arvensis</i> L.	Kapselfrucht	0.05	sporadisch	0.00	-	2.41	rezedent
Rhamnaceae	<i>Paliurus spina-christi</i> Mill.	Steinfrucht	0.00	-	0.03	sporadisch	0.00	-
Rubiaceae	<i>Sherardia arvensis</i> L.	Kelch	0.17	sporadisch	0.05	sporadisch	0.34	subrezent
Rubiaceae	<i>Sherardia arvensis</i> L.	Teilfrucht	0.01	sporadisch	0.00	-	0.00	-

Auf Fläche II war die Evenness mit 0.2 und der Shannon-Index mit 1.3 wesentlich niedriger als mit 2.3 auf Fläche I und mit 2.4 auf III. Das Abfallmaterial der Untersuchungsflächen I und III verzeichnete somit eine höhere Diversität an Pflanzenarten als jenes von Fläche II (Tab. 3).

Tab. 3: Biodiversitätsindices der untersuchten Standorte. Individuenzahl (N), Artenzahl (S), Diversitätsindex nach Shannon-Weaver (H'), maximal möglicher Diversitätswert (H_{max}) und die Evenness (E), d.h. der Ausbildungsgrad der Diversität der Pflanzenarten im Abfallmaterial der Untersuchungsflächen. — Tab. 3: Biodiversity indices of the investigated sampling sites. Number of individuals (N), Species richness (S), Dominance index (d), Shannon-Weaver diversity index (H'), maximum diversity of species which could possibly occur (H_{max}) and Evenness (E) of plant species in chaff piles of the respective sampling sites.

Untersuchungsfläche	N	S	H'	H _{max}	E
Cres Nord	6151	42	2.3	5.4	0.4
Cres Mitte	4737	43	1.3	5.4	0.2
Cres Süd	9815	26	2.4	4.7	0.5

Der Jaccard Index ergibt nur etwa ein Drittel Übereinstimmung im Spektrum der gefundenen Pflanzenarten im Abfallmaterial der Untersuchungsflächen (Tab. 4).

Tab. 4: Jaccard Index. — Tab. 4: Jaccard index.

Untersuchungsfläche	I	II
Cres Nord		
Cres Mitte	28.89	
Cres Süd	36.17	37.93

Im Abfallmaterial auftretende Diasporen und Pflanzenteile:

In den Probenahmen auf Fläche I wurde eine Gesamtanzahl von 6.151 Diasporen und Pflanzenteile identifiziert; Probenahmen auf Fläche II umfassten 4.737 Diasporen und Pflanzenteile; Proben auf Fläche III setzten sich aus 9.815 Diasporen und anderen Pflanzenteilen zusammen. Insgesamt wurden 21 Typen pflanzlicher Diasporen und Pflanzenteile im Abfallmaterial nachgewiesen (Abb. 5). Vornehmlich wurden folgende Typen verzeichnet:

- Auf Teilfrüchte entfiel im Abfallmaterial mit einem Prozentanteil von 34% der größte Anteil. Häufig wurden Teilfrüchte von *Zacintha verrucosa* Gaertn. (Asteraceae), *Crepis verrucosa* Gaertn (Asteraceae), *Scorpiurus muricatus* L. (Fabaceae), *Erodium cicutarium* L. (Geraniaceae) und gelegentlich von *Salvia officinalis* L. (Lamiaceae) gefunden.
- Hülsen kamen mit einem Anteil von 17.2% vor. Am häufigsten traten Hülsen von *Medicago minima* L. (Fabaceae) auf, gefolgt von *Medicago rigidula* (L.) (Fabaceae), gelegentlich auch von *Medicago arabica* L. (Fabaceae), *Lotus corniculatus* L. (Fabaceae), *Anthyllis vulneraria* L. (Fabaceae), *Medicago carstiensis* L. (Fabaceae) und *Astragalus hamosus* L. (Fabaceae).

- Mit einem Anteil von 9.5% wurden Petale von *Trifolium campestre* Schreb. am dritthäufigsten im Abfallmaterial nachgewiesen.
- Auf Kelche entfiel ein Anteil von 9.2%. Quantitativ am häufigsten vertreten waren Kelche von *Anthyllis vulneraria* L. (Fabaceae), *Trifolium angustifolium* L. (Fabaceae), *Trifolium scabrum* L. (Fabaceae), *Trifolium stellatum* L. (Fabaceae), *Marrubium vulgare* L. (Lamiaceae), *Thymus vulgaris* L. (Lamiaceae), *Salvia verbenacea* L. (Lamiaceae) und *Linum austriacum* L. (Linaceae).
- Ährchen waren mit einem Anteil von 7.9% vertreten. Am zahlreichsten wurden Ährchen von *Aegilops neglecta* Req. (Poaceae), *Dasyphyrum villosus* (L.) Borbás (Poaceae) und *Avena sterilis* L. (Poaceae) gefunden, gefolgt von *Cynosurus echinatus* L. (Poaceae), *Anthoxanthum odoratum* L. (Poaceae), *Aegilops triuncialis* L. (Poaceae), *Melica ciliata* L. (Poaceae) und *Vulpia ciliata* Dumort. (Poaceae).
- Samen waren im Abfall mit 7.5% Häufigkeit vertreten; am zahlreichsten von *Convolvulus althaeoides* L. (Convolvulaceae), mit nur einem geringen Anteil von *Euphorbia wulfenii* Hoppe (Euphorbiaceae).
- Achänen machten einem Anteil von 4.6% aus. Vornehmlich traten Achänen folgender Arten auf: *Carduus pycnocephalus* L., *Carthamus lanatus* L., *Scolymus hispanicus* L. (Asteraceae) und *Urospermum picroides* L. (Cichoriaceae).

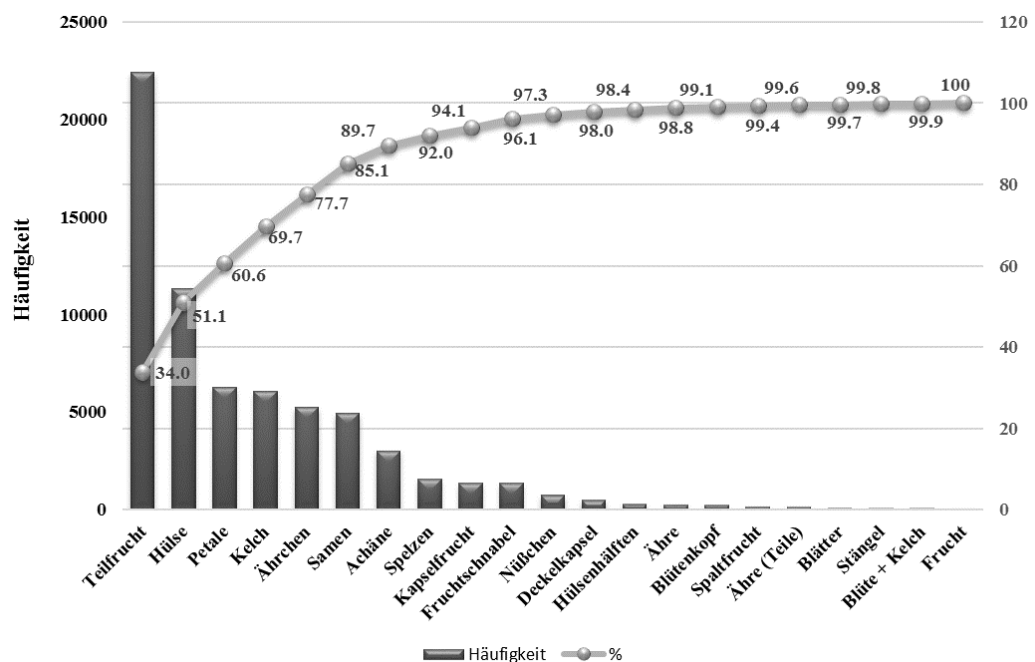


Abb. 5: Pareto - Diagramm zu den relativen Häufigkeiten (%) der Diasporen und Pflanzenteile im Abfallmaterial. — Fig. 5: Pareto - diagramm of the relative frequency (%) of propagule types and plant parts that occurred in chaff piles.

Diskussion

Beschreibung und Vermessung der Nestoberflächen

Die Tatsache, dass Ernteameisen die Nestoberflächen vegetationsfrei halten, hat zu zahlreichen, z.T. spekulativen Hypothesen geführt. Nach einer gängigen Interpretation fungieren die vegetationsfreien Nestoberflächen einerseits als Hitzeabsorber, andererseits würden Pflanzen unwillkommenen Schatten spenden und gleichzeitig dem Boden Feuchtigkeit entziehen (WHEELER & WHEELER 1986, RISSING 1988, BUCY & BREED 2006, CAPINERA 2008). Zusätzlich könnten Wurzeln die Nestarchitektur wie Gänge und Kammern zerstören (WU 1990). Darüber hinaus könnten vegetationsfreie Nestoberflächen als Landeplatz für fliegende Männchen auf Hochzeitsflug dienen. Weiters könnte die schnelle Fortbewegung für Arbeiterinnen auf kahlen Nestoberflächen erleichtert werden (FEWELL 1988). Ähnlich wie bei Arten der Ernteameisengattung *Pogonomyrmex* könnten *M. wasmanni* - Kolonien Pflanzen von der Nestoberfläche als Reaktion gegen Ameisen jagende Spinnen entfernen um den Bau von Spinnennetzen in der Vegetation direkt über den Nestern zu verhindern (MACKAY 1982).

Abfallmaterial

Eine mitteleuropäische *Messor*-Kolonie sammelt täglich bis zu 27.000 Pflanzensamen, überwiegend Getreidekörner, ein. In einer 4-monatigen Erntezeit ergibt das ca. 12 kg (VEILE 1991). Die Analyse des Abfallmaterials der mediterranen Ernteameise *M. wasmanni* zeigte deutlich ein reichhaltiges Spektrum an Pflanzenarten, allerdings ergab der Jaccard Index im Vergleich der nachgewiesenen Pflanzenarten im Abfallmaterial aus dem Norden, der Mitte und aus dem Süden des Verbreitungsgebietes auf Cres nur etwa ein Drittel an Übereinstimmung. Darüber hinaus belegen die Ergebnisse, dass nur von wenigen Pflanzenarten Samen, Diasporen, sowie Pflanzenteile in größeren Mengen eingetragen wurden. Im Abfallmaterial traten lediglich zwei eudominante und vier dominante Pflanzenarten auf. In einer physisch belastenden Umwelt, in welcher mediterrane Ernteameisen vorkommen, produzieren nur wenige Pflanzenarten ausreichend Samen zur Deckung des Nahrungsbedarfes. Die ökologische Bedeutung eines weiten Spektrums an Nahrungspflanzen wird auch durch eine Feldstudie an *Messor rufitarsis* Fabricius, 1804, welche in weiten Teilen Zentraleuropas vorkommt, unterstützt (HAHN & MASCHWITZ 1985). Im Abfallmaterial von *M. wasmanni* Kolonien wurden insgesamt 21 Typen pflanzlicher Diasporen und Pflanzenteile identifiziert. Vornehmlich setzte sich das Abfallmaterial aus Teilfrüchten von *Zacintha verrucosa* Gaertn. (Asteraceae) und *Erodium cicutarium* L. (Geraniaceae), Hülsen von *Medicago minima* L. (Fabaceae) und *Trigonella corniculata* L. (Fabaceae) sowie aus Petalen von *Trifolium campestre* Schreb. (Fabaceae) zusammen. Darüber hinaus wurden im Abfallmaterial Kelche diverser Arten der Familien Fabaceae und Lamiaceae gefunden. Dieses Ergebnis stimmt mit der Ernährungsweise granivorer Ernteameisen der Gattungen *Pheidole* Westwood, 1839, *Monomorium* Mayr, 1855, *Pogonomyrmex* Mayr, 1868 und *Messor* (ANDERSEN 1991) überein. Granivore Ernteameisen sammeln Samen, andere Diasporen und Pflanzenteile ein, wobei die Spreu von den Samen erst im Nest getrennt wird und nur Samen zu Ameisenbrot, weiterverarbeitet werden. Dieses stellt die Nahrung von *M. wasmanni* dar. Nicht als Nahrung verwertbare Pflanzenteile werden aus dem Nest ausgetragen (HÖLLDOBLER & WILSON 1990, VEILE 1991) und an der Nestoberfläche angehäuft (Abfallmaterial). Wenn das Angebot bevorzugter Samen und Früchte gering ist, sammeln Ameisen auch weniger begehrte Pflanzenteile, wie Petale, Blütenteile, Kelche, Blätter und Stängel ein (RISSING & WHEELER 1976). Zusätzlich wurden im Abfallmaterial von *M. wasmanni* Kolonien große Mengen an intakten, jedoch nicht ausgekeimten Samen festgestellt (Abb. 5). Dieser Befund unterstreicht die Tatsache, dass *M. wasmanni* Ernteameisen, trotz ihrer granivoren Ernährungsweise auch eine bedeutende Funktion in der Samenverbreitung einnehmen

(HÖLLDOBLER & WILSON 1990). Im Gegensatz dazu tragen beispielsweise *Formica rufa* Linnaeus, 1761 Arbeiterinnen Diasporen aufgrund ihrer Elaiosomen in das Nest ein. Dort trennen sie Elaiosomen von den Samen ab und entfernen anschließend die Samen, für die sie keine Verwendung haben, aus dem Nest. Elaiosomen sind als lock- und nährstoffhaltige Anhängsel an Samen und anderen Diasporen für viele Ameisenarten, besonders für zahlreiche Gattungen der Myrmicinae, sehr attraktiv (SEIFERT 2007). Elaiosomen können an verschiedenen Samenteilen oder Nußfrüchtchen ausgebildet werden. Sie allein sind für den Verzehr bestimmt, und werden oft schon auf dem Weg zum Nest abgebissen. Die Samen dieser sogenannten „Myrmecochoren“ (RIDLEY 1930) bleiben unterwegs liegen und kommen so zur Keimung und Verbreitung.

Obwohl sich Ernteameisen der Gattung *Messor* hauptsächlich oder ausschließlich von Pflanzensamen ernähren (Granivorie) (SHEATA & KASCHEF 1971, LEVIEUX & DIOMANDE 1978, ONOYAMA & ABE 1982, HAHN & MASCHWITZ 1985, CERDÁ & RETANA 1994, DETRAIN & PASTEELS 2000 und HENSEN 2002), konsumieren sie gelegentlich auch Insekten, Faeces und Schnecken (AZCÁRATE et al. 2005 und PÁLL-GERGELY & SÓLYMOS 2009). Eine Analyse des von *M. wasmanni* Arbeiterinnen eingetragenen Materials weist ebenfalls auf den gelegentlichen Verzehr von tierischen Überresten hin (TRAXLER 2016a). Die größten Mengen an eingetragenen tierischem Material fanden sich im Frühsommer (Mai), wo es einen Anteil von 2,6% von der Gesamtmenge des eingetragenen Materials ausmachte. Im Juli-August umfasste der tierische Anteil lediglich 0,6% und im Oktober 0,7% (TRAXLER 2016a). Eine Studie von AZCÁRATE et al. 2005 an der Ernteameise *M. barbarus* weist darauf hin, dass der gelegentliche Verzehr von Insekten und Schnecken eine zusätzliche Proteinquelle darstellt, wenn pflanzliche Nahrung, beispielsweise im Frühjahr, in noch ungenügender Menge zur Verfügung steht oder während länger andauernden Dürreperioden stark reduziert wird bzw. wenn Ameisenkolonien aufgrund von Fressfeinden ihre Aktivitäten außerhalb des Nestes einstellen und die Nesteingänge verschließen (Traxler 2016b).

Zusammenfassung

Die Untersuchung von *M. wasmanni* Ernteameisen Kolonien auf der kroatischen Insel Cres erfolgte vom 28. 05. 2009 bis 24. 10. 2009. Das pflanzliche Material im Abfallmaterial von *M. wasmanni* – Kolonien umfasste einen Gesamtanteil von 90.9%. Der restliche Anteil von 9.1% setzte sich aus tierischen Überresten und Orthoptera-Faeces zusammen. Es wurde ein reichhaltiges Spektrum an Nahrungspflanzen identifiziert, welches insgesamt 55 Pflanzenarten aus 20 Familien umfasste. Zusätzlich wurden zahlreiche tierische Taxa erfasst. Gastropoda dominierten mit 53% relativer Häufigkeit im tierischen Material, Coleoptera repräsentierten mit 38% relativer Häufigkeit die zweithäufigste Tiergruppe. Ergebnisse zeigen, dass nur wenige Pflanzenarten Samen, Diasporen, sowie Pflanzenteile in größeren Mengen eingetragen wurden. Es traten lediglich zwei eudominante und vier dominante Pflanzenarten auf im Abfallmaterial auf. Darüber hinaus zeigte die Zusammensetzung der nachgewiesenen Pflanzenarten im Abfallmaterial aus dem Norden, der Mitte und aus dem Süden des Verbreitungsgebietes auf Cres nur etwa ein Drittel an Übereinstimmung. Insgesamt konnten 21 Typen pflanzlicher Diasporen und Pflanzenteile nachgewiesen werden. Vornehmlich setzte sich das Abfallmaterial aus Teilfrüchten, Hülsen, Petalen, Kelchen, Ährchen, Samen sowie Achänen zusammen. Der hohe Anteil von noch intakten, keimfähigen Samen (7.5%) im Abfallmaterial weist darauf hin, dass *M. wasmanni* - Kolonien trotz ihrer weitgehend granivoren Ernährungsweise auch eine bedeutende Funktion in der Samenverbreitung einnehmen. Der gelegentliche Verzehr von Insekten und Schnecken stellt eine zusätzliche Proteinquelle dar, wenn pflanzliche Nahrung, beispielsweise im Frühjahr oder während länger andauernden Dürreperioden in ungenügendem Ausmaß verfügbar ist. Darüber hinaus halten *M. wasmanni* - Kolonien ihre Nestoberflächen frei von Vegetation. Der Grund bleibt jedoch noch ungeklärt.

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6.3. Paper II

Traxler T. (2016) The impact of predation by the myrmecophagous spider *Zodarion elegans* (Araneae: Zodariidae) on the activity pattern of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae). *Ecologica Montenegrina*, 7: 328-344.



Foto by T. Traxler

The impact of predation by the myrmecophagous spider *Zodarion elegans* (Araneae: Zodariidae) on the activity pattern of the Mediterranean harvester ant *Messor wasmanni* (Hymenoptera: Formicidae)

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Abstract

This study was designed to determine the effect of predation by the zodariid, obligate myrmecophagous spider *Zodarion elegans* (Simon, 1873) on the activity pattern and behavior of the Mediterranean harvester ant *Messor wasmanni* Krausse, 1910. Previous field studies suggested that the activity patterns of *M. wasmanni* colonies are modified not only by microclimatic conditions, but also by biological factors such as the presence of predators. The present study clearly demonstrates that *M. wasmanni* colonies respond in two different ways to spider predation. The ants 1) attack the invader, and 2) temporarily stop all foraging activities and close nest entrances with pebbles and other materials. This causes obligate myrmecophagous spiders such as *Z. elegans* to leave such inactive colonies and move to active ones nearby. Moreover, the laboratory experiments show that the capture of a single ant is in every case sufficient to trigger cessation of foraging activities and nest closure. After the spider attacks, entrances remained closed for up to six days. Perturbation experiments show that events that directly affect workers engaged in one task outside the nest also alter the activity intensity of task performance inside the nest. All exterior workers remain inside the nest when entrances are closed. Inside the nest, only a small proportion of marked foragers switch to food processing, while the majority was inactive or performed grooming during the inactive phase outside the nest.

Key words: myrmecophagy; activity pattern; ant-eating spider; nest closure.

Introduction

Spiders represent a key group of terrestrial arthropod predators present in numerous habitats (Givens 1978). Of the approx. 44,900 known species of spiders (Platnick 2014), most are averse to ant predation because ants can be dangerous prey even though they provide a rich source of nourishment (Pekár 2004). Ants are able to recognize each other, turn aggressive toward intruders (Cushing 2012) and may confront them with bites from powerful mandibles (Patek *et al.* 2006), stings, formic acid and other defensive chemicals. Additionally, ants are highly agile; they can mount a communal attack and are so numerous that it is difficult to avoid encountering them (Hölldobler & Wilson 1990). For spiders, myrmecophagy can be a hazardous

strategy. Some spiders have adapted ant-specific capture techniques (Castanho & Oliveira 1997) and favor ants over other types of prey. Sporadically, myrmecophagous spiders lose limbs to ants (Glatz 1967). The dietary specialization of spiders ranges from euryphagic to stenophagic (Huseynov *et al.* 2008). Over 100 species of spiders in several families subsist partially on ants (Cushing 2012), e.g., Oecobiidae (Glatz 1967), Salticidae (Li *et al.* 1996; Jackson *et al.* 1998), Theridiidae (MacKay 1982; Porter & Eastmond 1982), Gnaphosidae (Boevé 1992) and Zodariidae (Glatz 1967; Pekár 2004, 2009; Pekár *et al.* 2005). The myrmecophagous spider investigated in this study belongs to the Zodariidae, one of the most diversified families of spiders (Platnick 2014). Information on predatory behavior and prey is available for only eight of 74 zodariid genera (Jocqué 1991), namely *Lachesana* Strand, 1932; *Lutica* Marx, 1891; *Habronestes* L. Koch, 1872; *Psammoduon* Jocqué, 1991; *Diores* Simon, 1893; *Trygetus* Simon, 1882; *Zodariellum* Andreeva & Tyschchenko, 1968 and *Zodarion* Walckenaer, 1826 (Jocqué & Dippenaar-Schoeman 1992; Ramirez 1995; Allan *et al.* 1996; Rössl & Henschel 1999; Pekár *et al.* 2005). The first four genera belong to “ancestral” zodariids, which are apparently polyphagous and are considered plesiomorphic (Pekár & Lubin 2009). The latter four genera belong to the Zodariinae subfamily, which are presumably myrmecophagous or termitophagous (Jocqué 1991). Pekár (2004) hypothesized that obligatory myrmecophagy is a derived behavior because it is present only in more recent taxa. These spiders are unable to subdue prey other than ants (Cushing 2012, Pekár & Toft 2014) and may actively and preferably choose ants as prey (Huseynov *et al.* 2008).

Non-web-building spiders, such as zodariids and salticids, typically use a specific capture strategy, namely the ‘bite-and-release’ tactic (Jackson & van Olphen 1992; Cushing & Santangelo 2002; Cushing 2012). It is characterized by an attacking and handling phase, followed by a waiting period at a safe distance (Pekár 2004). The attacking phase typically involves a very rapid lunge to the rear of the ant, followed by a bite in the most extended ant extremities, such as legs (Pekár 2004). The spider then retreats to a safe distance (Pekár 2004) and may repeat this procedure several times until the ant becomes paralyzed. Afterwards, the moribund ant is carried to a secluded place where the spider starts to feed (Cushing & Santangelo 2002). One probable advantage of this capture strategy, which limits contact between predator and prey, is that it enables the predator to avoid being injured or killed when ants counterattack (Pekár 2009).

According to MacKay (1982), ants respond to spider predation in four to five ways. They 1) move nest entrances; 2) post guards; 3) attack spiders; or 4) stop foraging and possibly close nest entrances (MacKay 1982). Additionally, as a reaction against ant-eating, web-building spiders, most species of the genus *Pogonomyrmex* Mayr, 1868, including *P. rugosus* Emery, 1895, 5) cut vegetation from the surface of the nest and from foraging trails to form well-defined open trails with widths of 5-10 cm (MacKay 1982).

Most empirical work on the activity pattern of harvester ants tends to emphasize interference competition (Gordon 1988) and microclimatic conditions as the most important predictors for colony activation and activity intensity (Cole *et al.* 2010; Belchior *et al.* 2012). It has been postulated that colonies of *Messor barbarus* (Linnaeus, 1767) become active after critical values of relative humidity and internal soil temperature have been reached (Azcarate *et al.* 2007).

Social insect colonies operate without any central control, i.e., no animal is in charge and any colony member directs the behavior of another (Gordon 2002). A single worker ant is unable to assess the needs of the colony. A key feature of the division of labor in insect colonies is its plasticity (Robinson 1992). Activities are interdependent: the numbers of workers engaged in one task depend on the number of workers engaged in another (Gordon 1987, 1989). As the needs of the colony change, e.g., as more larvae need to be fed and more resources become available and must be processed inside the nest, colonies adjust the numbers of workers engaged in each task (Gordon 2002). Workers switch from one task to another, although not all transitions are possible (Gordon & Goodwin 1992; Gordon 2002). A worker ant’s decision whether to perform a task depends primarily on cues about the physical state of the environment (Gordon 2002). For example, if chambers of the nest are damaged, then more workers are engaged in nest maintenance work. Task decisions also depend on social cues arising from interactions with other workers (Gordon 2002). Workers from different task groups meet each other as they enter and leave the nest. The rate at which one worker encounters others influences its task decisions. The pattern of interactions among workers as they move around can be interpreted as an ad hoc, dynamic network (Adler & Gordon 1992; Albert & Barabasi 2002).

Interior workers are a discrete subset of the colony. They rarely mix with exterior workers (Gentry 1974; Porter & Jorgensen 1981; MacKay 1983), who remain in the upper levels of the nest. Inside the nest,

PREDATION IMPACT BY ZODARION ELEGANS ON THE ACTIVITY PATTERN OF MESSOR WASMANNI

workers care for the brood (the preadult forms: eggs, larvae, and pupae); they feed nest mates and brood (trophallaxis); they groom themselves and their nest mates; they process and store seeds, construct and maintain chambers, or simply remain motionless and perform no recognizable task (MacKay 1983). Workers that are engaged in activities outside the nests form a distinct group and are apparently older than interior workers (Gordon 2002). Activities such as foraging, searching for and retrieving food, patrolling, assessing the food supply, midden work, and sorting the colony refuse pile are performed outside the nest (Gordon 2002).

The hypothesis, which is proposed here, is that activity patterns are influenced not only by microclimatic conditions (Ruano *et al.* 2000; Azcárate *et al.* 2007; Cole *et al.* 2010) and interference competition (Cerdá *et al.* 1998; Bestelmeyer 2000; Sanders & Gordon 2000), but also by predation. Which factor is the most significant in triggering these activity patterns remains open.

I then examined whether perturbations such as predation pressure by the myrmecophagous spider *Zodarion elegans* (Simon, 1873) affect activities inside the nest as well.

The following aspects were investigated under laboratory conditions:

1. Closure of entrances subject to the presence of *Z. elegans*;
2. Foraging activity subject to the presence/absence of *Z. elegans*;
3. Relationship between the duration of aboveground activity (h/day) of *Messor wasmanni* Krausse, 1910 workers and the presence/absence of *Z. elegans*;
4. The effect of spider predation pressure on activities inside the nest.

Material and Methods

Field work

Study site and study organisms

The western and southern areas of Cres, SSW to the peninsula of Istria, have Mediterranean climate. The north is characterized by the sub-Mediterranean (hardwood) type with deciduous forests (Rikli 1943; Horvat *et al.* 1974).

The harvester ant *M. wasmanni* is a common seed predator in Mediterranean grasslands of southern Europe (Bračko *et al.* 2014). The nests can be easily detected in the field by clearly defined networks of trunk trails.

Spiders of the genus *Zodarion* occur in open, sparsely vegetated habitats from Western Europe to central Asia and were introduced to the USA (Jocqué 1991; Platnick 2014). *Zodarion elegans* hides during the day in igloo-shaped retreats covered with small sticks or pebbles, which are under stones and other hard substrate (Jocqué 1991; Pekár & Křál 2001). Like other members of this genus, this myrmecophagous spider uses a typical “bite-and-release” prey capture tactic (Cushing & Santangelo 2002).

Data collection

Field work was carried out close to Zaglav, a small village on Cres, Croatia (44° 48' 21.1" N, 14° 21' 53.2" E). Activity patterns and microclimatic conditions were measured in May 2008 and May, August and October 2009 for five days, in each case every half-hour throughout the day between 04:30 AM and 22:30 PM. Six colonies in May 2008, eight colonies in May 2009, five colonies in August 2009, and three colonies in October 2009 have been observed. To avoid repeated data taking, each colony was evaluated only once during field studies.

Activity pattern

The daily activity pattern of *M. wasmanni* as related to the presence of *Z. elegans* was investigated. Every half-hour, the number of *M. wasmanni* workers leaving and returning to the nest was counted within the duration of one min. Simultaneously, the microclimatic conditions (surface temperature and relative humidity) were recorded.

Nest closure

When aboveground foraging activity ceased, the duration until closure of the nest and the kind of materials used to close the nest were documented. *M. wasmanni* workers are weakly polymorphic, and size classes

(major-, medium- and minor-workers) were therefore taken into account. The presence of size classes led to an examination of whether the phenomenon of polyethism was evident. The number of collaborating workers was counted at 10-min intervals.

*Frequency of *Z. elegans**

The relative frequency of *Z. elegans* at active/inactive colonies and in chaff piles was recorded in May, August and October 2009. Each colony was included in the field studies only once to avoid repeated measurements. Nine active and seven inactive colonies in May 2009, nine active and eight inactive colonies in August 2009 and nine active and six inactive colonies in October 2009 have been observed.

Microclimatic measurements

Surface temperature and surface relative humidity were measured for all investigated colonies every half-hour using a PT 100 Testoterm 0.1°C precision thermometer and a PT 100 Testoterm 0.1% precision thermohygrometer. All measurements were taken at a distance of 10 cm from the nest entrances. The first data were taken in the morning before the colonies became active. Measurements continued to be taken during the activity period and were completed when the colonies ceased activity. As a precaution, the sensors were protected from direct sun radiation.

Laboratory investigation

In May 2009, a *M. wasmanni* colony was transferred from an area where *Z. elegans* naturally occurs to a formicarium in the laboratory. In August 2009, 10 mature *Z. elegans* individuals (five males, five females) were collected by hand in the same area (near Martinšćica). In the laboratory, each spider was put in a glass tube (17 mm x 60 mm) with soil substrate at the bottom.

Perturbation experiment: closure of nest entrances in response to predation

To avoid a possible saturation effect on the predatory behavior of spiders, the individuals were starved for at least eight days prior to the experiments. During this time, most of the spiders built igloo-shaped retreats. For the experiments, each spider was prompted out of its retreat using a fine brush and then released into the formicarium. If the spider did not capture an ant after the first 15 min, the experiment was terminated and the spider was placed back into its glass tube. In case of a capture, the spider remained in the formicarium for at least 20 days, and in case of a repeated capture, the experiment was prolonged up to 30 days. Four perturbation experiments were carried out.

Effect of predation on activities inside the nest

Following Hölldobler & Wilson (1990), the number of behavioral acts recorded during the counts is used as sample size (N). The activities inside the nest that I have chosen to focus on in this study are listed in Table 1. All observations started on the first day after nest entrances were closed. In the formicarium, nine chambers were monitored. Every observed activity was noted along with the physical size class of the worker ant (minor-, medium- and major-worker). Workers were counted at two-hour intervals throughout the day, yielding a total of twelve counts per day. During the count, the laboratory was darkened. Ants are unable to perceive red light. Accordingly, the glass panes through which the ants are visible in the individual chambers were covered with red foil. Additionally, red light was used when counting ants in the chambers.

During the first experiment, entrances remained closed for up to three days, in the second experiment they remained closed for two days, in the third experiment for up to six days, and in the fourth experiment for up to three days (Table 2). The analyses included experiments one, three and four based on the assumption that the effect of predation increases the longer the entrances stayed closed. Per experiment, counts were performed at three consecutive days, yielding a total of nine observation days. To enable a comparison between the behavior under disturbed conditions (predator present in the formicarium) and under undisturbed conditions (no predator in the formicarium), the same observation procedure was repeated, but without a predator in the formicarium. The observation period under undisturbed conditions lasted 30 days.

For each activity listed in Table 1, the following calculation was carried out: to calculate the average value per day, the total number of times a certain activity was performed per physical size class over the observation period (nine days under disturbed conditions and 30 days under undisturbed conditions) was divided by the sum of observation days. Thereafter, the average value per day was divided by the percentage

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share of the respective size class (major-, medium-, minor-workers). The laboratory colony consisted of 6% major-workers, 18% medium-workers and 76% minor-workers. A Wilcoxon matched-pairs signed rank test was used as a non-parametric test to calculate if there is an effect of spider predation on the number of ant workers performing specific activities inside the nest. Data were not assumed to be normally distributed.

Table 1. Description of the analyzed activity types inside the nest.

Activity	Behavior
Inactivity	Ants remaining motionless inside the nest.
Patrolling	Ants running around in the nest in an apparently aimless manner.
Nest maintenance	Ants carrying nest material inside the nest; ants coming out of the nest and putting the nest material down in the nest yard and returning into the nest. Ants closing nest entrances.
Carrying food	Ants carrying seeds, fruits, plant material and parts of dead cockroaches inside the nest.
Food processing	Workers mostly perform food processing in small groups, consisting on average of two to four individuals.
Trophallaxis	The mutual transfer or exchange of regurgitated liquid food between adult ants and between adults and larvae.
Brood care	Ants cleaning eggs, larvae and pupae; adult ants feeding larvae.
Self-grooming	Ants cleaning themselves.
Allo-grooming	Ants cleaning each other. Sometimes one ant is cleaned by one to two workers; the one being groomed remains motionless.

Marked foragers

Prior to each perturbation experiment, 10 foragers per size class returning to the nest along the foraging trail and additionally carrying a seed or other food item were collected. Ants were marked with waterproof touch-up stick and were returned to the colony within two h. Each size class was assigned a unique color of paint, and ants were marked according to their size. Observations started on the first day after nest entrances were closed. Again, every observed activity was noted along with the physical size class of the marked ant. Observations were made at two-hour intervals throughout the day, yielding a total of 12 observations per day. Only 3-4 out of 10 minor-workers, 4-5 out of 10 medium-workers and 2-3 out of 10 major-workers were still alive at the end of experiments.

Ant morphology

Behaviors related to the respective worker size were examined by measuring the head width of minor-, medium- and major-workers. Ants were measured across the eyes to determine the average head widths. The head widths were measured with 0.01 mm accuracy using a Nikon stereomicroscope fitted with an ocular micrometer. Head widths were obtained to assess the presence of physically distinct size classes (Wilson 1953). Thirty workers per size class were taken from the laboratory colony after experiments were terminated.

Statistics

For the statistical analysis of the data the softwares SPSS Statistics 23 and GraphPad Prism 5 were used with a significance level of $p < 0.05$.

A linear regression analysis was applied to analyze the dependency of ant aboveground activity to surface temperature and surface relative humidity from May 2009 to October 2009. In all analyses, the dependent variable was the number of workers leaving the nest, and the two independent variables were soil temperature and relative humidity. All statistical tests were two-tailed.

The relative frequency of *Z. elegans* individuals found within a distance of max. 0.5 m to active/inactive ant colonies was investigated with an unpaired t-test. The relationship between the duration of

aboveground activity (h/day) of *M. wasmanni* workers and the presence/absence of *Z. elegans* was analyzed using a two-sample t-test. In addition, the following statistics were calculated: mean and SD for paralysis latency, size class distribution for ants involved in nest closure performed outside the nest, and the mean frequency of material used for entrance closure.

A Wilcoxon matched-pairs signed rank test was used as a non-parametric test to calculate if there is an effect of spider predation on the number of workers performing specific activities inside the nest. Data were not assumed to be normally distributed. All statistical tests were two-tailed.

Results

Field work

Activity pattern and microclimatic conditions

The daily foraging activity pattern of *M. wasmanni* colonies was strictly diurnal throughout the sampled seasons. In May 2009, the curves were clearly bimodal, with peaks in the morning and afternoon, in order to escape the high temperatures. No foraging activity was observed during the central h of the day (between 10:00 AM and 17:00 PM) when the soil surface temperature in the sun was 40°C. In summer and autumn, the foraging activity rhythm was also observed to change. The activity curve became unimodal in July/August 2009 and October 2009. Moreover, the number of h spent in aboveground activity per day varied considerably over the seasons (Table 2).

Table 2. Mean duration of aboveground activity (h) per day over the seasons.

Season	Mean±SD	N
May	5.20±1.53	5
July/August	4.25±0.35	2
October	10.15±1.92	3

Results from a linear regression analysis regarding the correlation between soil surface temperature, surface relative humidity and aboveground activity are shown in Table 3. Models based on data from May 2009 and July/August 2009 showed considerable lack-of-fit, which is indicated by low a R^2 of 0.084 and 0.024. The October 2009 model, however, satisfactorily explained 41.6% of the variance and was thus used as a basis for interpreting correlations. While soil temperature apparently has no impact on aboveground activity of *M. wasmanni*, relative humidity was significantly correlated with the aboveground activity. Both data on activity and data on inactivity per day were included in the calculation.

Table 3 Correlation between soil surface temperature, surface relative humidity and aboveground activity. In all analyses, the dependent variable was the number of ants leaving the nest. The two independent variables were soil surface temperature and relative humidity. The R^2 value explains how much of the variance (in percent) in the dependent variable can be explained by the independent variables. F: the F-test has the null hypothesis that there is no linear relationship between the two variables (in other words $R^2=0$). p: p indicates the statistical significance of the regression model; $p_{\text{soil temperature}}$ and $p_{\text{relative humidity}}$ indicate the statistical significance of the coefficients.

Season	ANOVA (Regression)			Coefficients	
	R^2	F	p	$p_{\text{soil temperature}}$	$p_{\text{relative humidity}}$
May	0.08	9.23	0.0001	0.50	0.0800
July/August	0.02	2.10	0.1260	0.10	0.0400
October	0.42	33.11	0.0001	0.53	0.0001

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Spider attack and nest closure

In 17 of the 22 field studies conducted from 2008 to 2009, *Z. elegans* was observed at *M. wasmanni* colony surfaces or foraging trails, or trying to dig into their closed nest entrances. On six occasions, the naturally occurring captures were observed. Immediately after being bitten by the spider, the ant became excited and moved around with opened mandibles and attacked both the surrounding area and the spider, which generally quickly fled to a safe distance. Other nest mates that passed by, antennated the attacked ant and, as a consequence, they became excited and started moving around with opened mandibles. Following a spider bite, the targeted ant began to stumble, its movements gradually decreased and the gaster bent under the mesosoma. This C-shaped body posture lasted for several min, after which the whole body became paralyzed. Paralysis latency ranged from 4.17–23.00 min (16.64 ± 7.82 , mean \pm SD; $N = 6$). Frequently (83.3%, $N = 5$), within min (3.62 ± 4.76 , mean \pm SD; $N = 5$) after the attack, spiders approached, stretched out their forelegs and palpated their prey. If the ant was still defensive, spiders retreated again. Spiders only started to feed on ants after immobilization, either directly at the location of the colony ($N = 4$) or they carried the paralyzed ants away from the nest to feed on them at a safe distance ($N = 2$).

The field studies revealed that *M. wasmanni* responded in two ways toward predation. 1) Sometimes ($N = 2$), major- or medium-workers attempted to chase away the spider. 2) Generally, ants terminated foraging activity for, at least, the day and closed entrances from the inside and outside using seeds, small leaves or twigs, and soil particles ($N = 17$). Nest closures occurred 41.7% ($N = 7$) in the evening, 17.7% ($N = 3$) at midday, and one colony (5.9%) closed at noon and again in the evening. A total of 35.3% ($N = 6$) of colonies ceased activity outside the nest and kept the entrances closed for the rest of the day. In the morning, workers quickly opened nest entrances from within and from outside and then began with aboveground foraging activities. Within an average of $50.50 \text{ min} \pm 47.27$ ($N = 12$) of nest opening, the foraging trail was established.

Ant size classes involved in nest closure

With termination of aboveground foraging activity, workers started to close entrances from both the inside and outside. Nest closure took on average 73.9 min ($N = 13$), but varied considerably (45–110 min). Nest closure was performed primarily by minor-workers (69.1%) (6.576 ± 11.35 ; mean \pm SD; $N = 822$), followed by medium-workers (24.6%) (2.344 ± 3.353 ; mean \pm SD; $N = 293$). With 6.2% (0.5920 ± 1.025 ; mean \pm SD; $N = 74$), major-workers contributed the smallest ratio of the total number of workers involved.

Frequency of Z. elegans

Fig. 1a-c shows that spiders leave the area of inactive ant colonies and move to nearby areas with active colonies. Spider density ranged from three to 10 spiders within a distance of max. 0.5 m to active colonies ($N = 27$) and from two to six individuals at inactive colonies ($N = 21$).

In May (spring) and August (summer), significantly fewer spiders were found in the immediate vicinity of inactive ant colonies compared with active colonies (Table 4). In October (autumn), probably due to inclement weather conditions, fewer spiders were recorded. No significant difference in the number of spiders between active and inactive colonies was observed.

Table 4. The relative frequency of *Z. elegans* individuals found within a distance of max. 0.5 m to active/inactive ant colonies. p: the p value is used to ask if there is a difference between the mean of two groups. t: to calculate a p value for an unpaired t test, first a t ratio is computed. The t ratio is the difference between sample means divided by the standard error of the difference, calculated by combining the SEMs of the two groups. df: degrees of freedom.

Month	p	t	df	Active colonies		Inactive colonies	
				Mean \pm SEM	N	Mean \pm SEM	N
May	0.0010	4.16	11.47	6.56 ± 0.77	9	3.00 ± 0.38	7
August	0.0001	5.38	12.15	7.22 ± 0.55	9	3.88 ± 0.3	8
October	0.1415	1.57	13.00	2.78 ± 0.32	9	2.00 ± 0.37	6

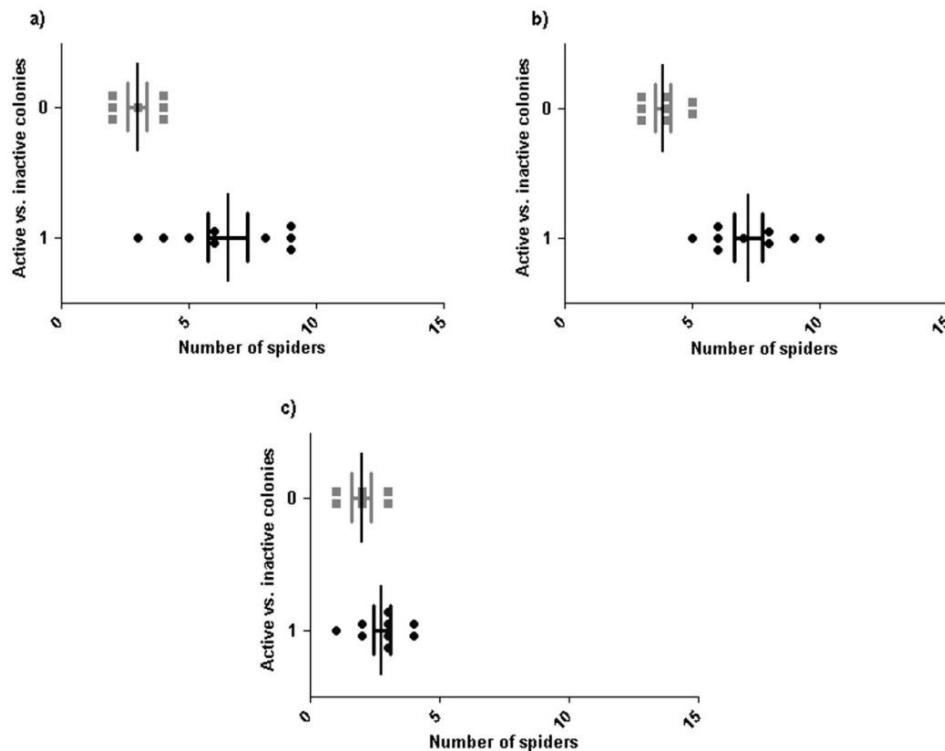


Figure 1. Frequency of *Z. elegans* individuals found within a distance of max. 0.5 m to active/inactive ant colonies in a) spring 2009, b) summer 2009 and c) autumn 2009 (1 = active colonies, 0 = inactive colonies).

Laboratory investigation

Ant morphology

Mean head widths of minor-, medium- and major-workers were significantly different using an one-way analysis of variance ($R^2 = 0.89$, $F = 367.8$, $P < 0.0001$). These data indicate that *M. wasmanni* workers are weakly polymorphic and show slight allometry with continuous size variation. Three arbitrarily demarcated size categories of workers in mature colonies were found: major-workers (head width: mean \pm SD = 2.38 ± 0.19 mm, $N = 30$), medium-workers (head width: mean \pm SD = 1.71 ± 0.25 mm, $N = 30$) and minor-workers (head width: mean \pm SD = 1.06 ± 0.10 mm, $N = 30$).

Perturbation experiment: closure of nest entrances in response to predation

Laboratory investigations were conducted to better grasp the parameters that lead to the closure of nest entrances. Fig. 2 shows that *Z. elegans* individuals were present in the formicarium 72% of the time of the total experiment (i.e., 100 days); in the remaining 18% of the time, spiders were absent and entrances were always kept open. Despite the presence of a spider in the formicarium, no ant was captured in 88.9% of the time (64 days). As a result, entrances remained open even after the end of aboveground activity. In 11.1% of the time (eight days), *Z. elegans* individuals captured a total of 15 ant workers. These observations suggest that one spider specimen captures no more than two, on average 1.9 ants per day (Table 5). Despite the low number of prey, the data in Fig. 2 indicate that a major effect of predation is observed on colony behavior. One captured worker ant is sufficient with 100% certainty to prompt the ants to close nest entrances after aboveground activity has stopped. In six of eight times, ants ceased aboveground activity and closed

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entrances for a period of up to six days (2.25 ± 1.83 , mean \pm SD) (Table 5). The period of complete nest closure could last for several days, and in four of eight times it was followed by a period of one to three days (1.38 ± 0.74 , mean \pm SD), in which the ants recommenced foraging in the daytime and afterwards closed the entrances at night. After an average of 4.17 ± 3.60 (mean \pm SD) days, the nests were completely reopened again, i.e., entrances were open day and night; although spiders were still present in the formicarium, no new prey was taken. When *Z. elegans* individuals were removed from the formicarium, ants no longer closed nest entrances after daytime foraging activity outside the nest.

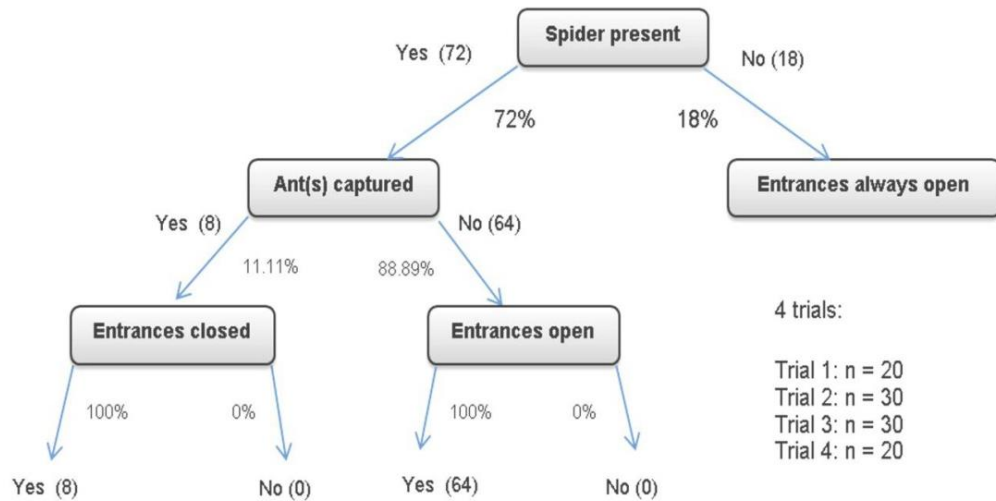


Figure 2 Flow diagram of nest entrance closure in response to prey capture by the spider *Z. elegans*. In total, four experiments were performed with an overall duration of 100 days (Trial 1: n = 20, Trial 2: n = 30, Trial 3: n = 30, Trial 4: n = 20, $n_{\text{total}} = 100$). The capture of *M. wasmanni* workers by *Z. elegans* is necessary to prompt ants to end aboveground activity and close nest entrances. By contrast, the presence of spiders in the formicarium alone was not sufficient to prompt ants to close nest entrances after aboveground foraging activity ceased.

Table 5. Duration of nest entrance closure after prey capture. Individual spiders capture on average 1.88 ants per day. In response to such predation, ants ceased aboveground foraging activity for an average of 2.25 days, or they closed nest entrances after daytime foraging activity. After up to three days, the ants reopened the nest entrances and kept them open for the duration of aboveground foraging activity.

Trial	Number of ants captured	Number of days		
		Nest is closed day and night	Nest is open in day and closed at night	Before nest reopens day and night
1	3	2	1	0
	1	3	2	8
2	2	2	1	2
	1	1	1	8
3	2	6	1	0
	1	3	1	6
4	3	0	3	0
Sum	18	18	11	25
Mean	1.875	2.250	1.375	4.167
SD	0.835	1.832	0.744	3.601

Foraging activity subject to the presence/absence of predators

Figs. 3 and 4 show a marked decrease in foraging activity (leaving and returning ants) when *Z. elegans* individuals were present in the formicarium during the first and fourth experiments. In contrast, trials two and three revealed exactly the opposite outcome; the activity considerably increased with predator presence. Hence, no conclusion can be drawn about whether aboveground activity decreases or increases in relation to predator presence.

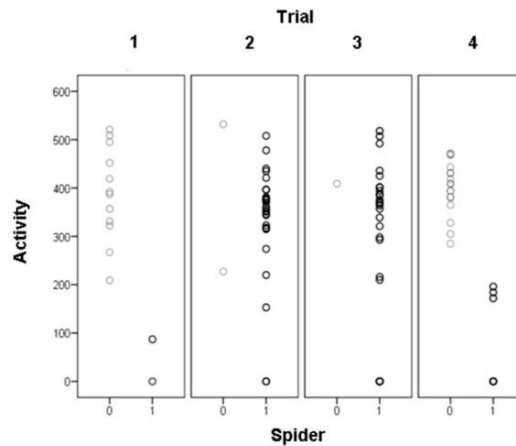


Figure 3 Foraging activity of ants leaving the nest in correlation with absence/presence of *Z. elegans* individuals. Activity per day was measured as the number of leaving plus returning worker ants per min in a half-hour intervals; counts were summarized per day (0 = absence of *Z. elegans*, 1 = presence of *Z. elegans*).

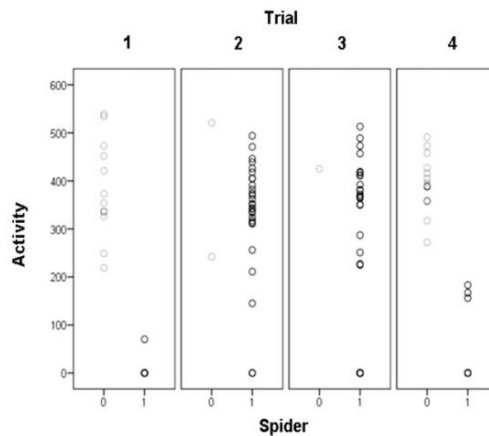


Figure. 4 Foraging activity of ants returning to the nest in correlation with absence/presence of *Z. elegans* individuals. Scores were taken during half-hour intervals (0 = absence of *Z. elegans*, 1 = presence of *Z. elegans*).

Duration of aboveground activity

Almost no difference was detected in the duration of aboveground activity of ant colonies in correlation to predator presence (14.63 ± 0.35 ; mean \pm SD; $N_{(\text{predator present})} = 55$) or absence (14.18 ± 0.49 ; mean \pm SD; $N_{(\text{predator absent})} = 28$) (p-value = 0.460). On a total of 17 days of observation, no aboveground activity was detected; data for these days were excluded from calculation.

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Effect of predation on activities inside the nest

The relative frequency of ant activities inside the nest changed in response to predation pressure outside the nest. A reciprocal relationship was evident between nest maintenance workers, who start to close nest entrances with pebbles and plant material in response to predation, and workers performing exterior activities such as patrolling, foraging and midden work. In these perturbation experiments, an increase in one activity was accompanied by a decrease in the others. Simultaneously, when foraging and other exterior activities decreased, nest maintenance workers started to close nest entrances. Thus, predation pressure impacted not only the activities outside the nest, but also inside the nest, causing widespread changes in the relative frequency of activities. This was true for the proportion of minor-workers involved in nest maintenance and for the number of workers performing activities such as self-groom, allo-groom, and trophallaxis, all of which increased significantly. In contrast, the number of inactive workers decreased significantly in all size classes in response to nest closure. Finally, the number of food-processing minor- and major-workers decreased as well (Table 6).

Table 6. The effect of spider predation on the number of ant workers performing specific activities inside the nest. Undisturbed conditions comprising 30 days of observation: N(minor) = 30,822, N(medium) = 7,464, N(major) = 2,302; disturbed conditions comprising nine days of observations: N(minor) = 7,950, N(medium) = 1,859, N(major) = 819. The average per day was calculated. The analysis examines if there is a difference in the number of workers performing one activity under undisturbed conditions and under disturbance (predation pressure). A Wilcoxon matched-pairs signed rank test was used as non-parametric test because data were not assumed to be normally distributed. W: sum of signed ranks. p: the p value is used to ask whether the difference between the mean of two groups is likely to be due to chance. *: p = 0.01 - 0.05, **: p = 0.001 - 0.01, ***: p ≤ 0.001.

Activity	Minor-workers		Medium-workers		Major-workers	
	W	p	W	p	W	p
Inactivity	72.00	**0.0024	78.00	***0.0005	62.00	*0.0122
Patrolling	0.00	1.0000	36.00	0.1763	3.00	0.9219
Nest maintenance	-	*0.0313	-	0.1250	20.00	0.1829
Carrying food	2.00	0.9527	35.00	0.0829	1.00	1.0000
Food processing	52.00	*0.0425	40.00	0.0830	46.00	*0.0452
Trophallaxis	-	**0.0015	-	***0.0005	43.00	*0.0273
	74.00		78.00			
Self-groom	-	***0.0010	-	**0.0049	-	**0.0086
	76.00		68.00		68.00	
Allo-groom	-	**0.0024	-	*0.0112	-	*0.0195
	72.00		58.00		39.00	
Brood care	-	0.3394	-	0.1514	-	0.1475
	26.00		38.00		34.00	

Marked foragers

One question was whether exterior workers also perform interior activities as a result of nest closure. Behavioral observations on marked foragers helped determine how flexible the response was to predation pressure. Under laboratory conditions, exterior workers comprised approximately 24% of the total adult *M. wasmanni* colony, with interior workers comprising the remainder. The tasks performed inside the nest by the marked foragers in the foraging area were – apart from inactivity and patrolling the interior of the nest – food processing, self-grooming and allo-grooming. Only a small proportion of the foragers switched to food processing, whereas the majority was either inactive, patrolling the interior of the nest or grooming (Fig. 5).

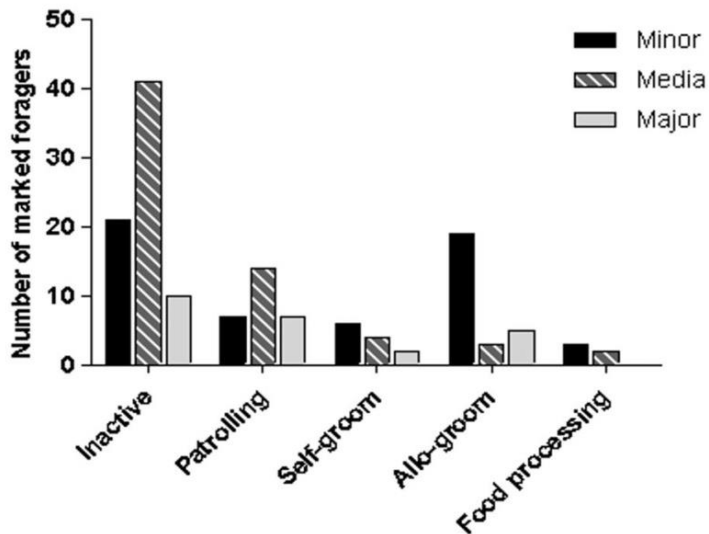


Figure 5. Tasks performed by marked foragers inside the nest when nest entrances were closed due to predation pressure. The number of workers per activity was summarized during the duration of three perturbation experiments. Per experiment 30 workers – 10 Minor-workers, 10 Medium-workers and 10 Major-workers – were marked.

Discussion

Activity pattern and microclimatic conditions

Surface temperature and surface relative humidity were not always significantly correlated with aboveground activity during the day (Traxler, unpublished). Nonetheless, the present results show a certain dependence of *M. wasmanni* colonies on microclimatic conditions. Colonies stopped aboveground activity at high daytime temperatures and simultaneous decreasing relative humidity. Crucial parameters for a restart of aboveground activity in the afternoon were decreasing temperature and increasing relative humidity. Nonetheless, in 28.3% of the total observations, colonies were not active at all during the day. These results suggest that the activity patterns of *M. wasmanni* colonies are not modified solely by microclimatic conditions (Ruano *et al.* 2000; Azcárate *et al.* 2007), but the biological factors, such as the presence of predators, may exert an influence (Whitford & Bryant 1979; Porter & Eastmond 1982).

The populations of the obligate myrmecophagous zodariid spider *Z. elegans* were mostly aggregated near *M. wasmanni* colonies. Individual spiders were often detected hiding among small stones next to the surface of ant nests, where their size and cryptic color pattern made them difficult to recognize. Zodariid spiders form igloo-shaped retreats by overlapping small pieces of debris (soil particles, rocks and plant material) on a silken framework using palps and front legs to manipulate the material (Jocqué 1991; Pekár & Křál 2001; Cushing & Santangelo 2002). This behavior is known in *Z. elegans* as well.

The results demonstrate that *Z. elegans*, like other zodariids (Pekár 2004), is a key predator on *M. wasmanni* harvester ants. *Zodarion elegans* showed the bite-and-release capture strategy typical for zodariid spiders. It was observed to carry paralyzed *M. wasmanni* workers with its chelicerae and thus pass unnoticed by approaching ants. This is a special form of deceptive behavior, in which the spider taps the antennae of the approaching ants with its front legs, thus imitating an important tactile cue for ant nest mate recognition. These observations correspond well with those made by Pekár & Křál (2002) on *Zodarion rubidium* Simon, 1914 and *Z. germanicum* (C. L. Koch, 1837).

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Reaction of ants to predation

Messor wasmanni colonies demonstrated two responses to spider predation. 1) They attack the predator, e.g., *M. wasmanni* workers (medium-, major-) drove *Z. elegans* spiders away from the vicinity of their colony. This is an effective strategy against spiders such as *Z. elegans*, which do not utilize silk in prey capture. However, this defense requires size polymorphism in ant workers. The present results show that *M. wasmanni* workers are weakly polymorphic and show slight allometry with continuous size variation. Only larger *M. wasmanni* workers (medium-, major-) successfully repelled *Z. elegans* attacks. 2) They cease foraging and close nest entrances. The field studies showed that *M. wasmanni* colonies respond to predation by reducing all aboveground activity. In such cases, nest entrances remained closed for the entire day or longer. The response of harvester ant colonies to predation may be great, yet the rate of ant mortality may be low (MacKay 1982). The laboratory experiments support the hypothesis that *M. wasmanni* temporarily stops foraging and close nest entrances in response to predation. Conversely, workers never closed nest entrances in the absence of *Z. elegans* in the formicarium. The capture of only a single ant is sufficient to trigger nest closure definitively, which occurs after the end of aboveground activity. Subsequently, entrances remained closed for a maximum of six days. Within 24 h after the removal of *Z. elegans* individuals from the formicarium, ants became active again aboveground. It has been noted that the mere presence of *Z. elegans* in the formicarium was not sufficient to cause nest closure (Fig. 2). Previously, Gordon (1986) detected a decline in aboveground activity, which would theoretically prevent the entire colony from being destroyed by predation (Gentry 1974). In the present formicarium experiments, however, *M. wasmanni* showed no significant correlation in the intensity of aboveground activity or in the time spent foraging per day with respect to the presence or absence of *Z. elegans*. Under laboratory conditions, *M. wasmanni* entirely halts foraging activity and closes the nest entrances only in response to a predation event. Apparently, *Z. elegans* activity can alter the activity pattern of *M. wasmanni*. Further examples for nest closures are known in a range of species in the genera *Pogonomyrmex* (Hölldobler 1970; Gentry 1974; MacKay 1982; Johnson 2001) and *Messor* Forel, 1890 (Traxler, unpublished).

Frequency of Z. elegans

The colonies of *Messor* spp. and *Pogonomyrmex* spp. have numerous burrows directly beneath the ground surface, filled with abundant seed reserves (Gentry 1974). It is therefore presumed that they can survive extended periods without seed intake, enabling colonies to replace lost ants and regain original strength (Gentry 1974). MacKay (1982) noted for *Pogonomyrmex rugosus* that cessation of aboveground activity and closure of nest entrances is probably the “cheapest” response with respect to metabolic cost and time, although it results in loss of food intake. It is assumed that the obligate myrmecophagous spider *Z. elegans* usually leaves the vicinity of inactive colonies and moves to active nests nearby. In spring and summer (but not in autumn, probably due to inclement weather and heavy rain), significantly more spiders were detected close to active versus inactive colonies. These observations correspond well with those made on the American harvester ants *Pogonomyrmex badius* (Latreille, 1802) and *P. rugosus*, which ceased foraging for seven to 10 days (Gentry 1974). MacKay (1982) calculated that if *P. rugosus* would continue foraging and if spider density did not change, then the nest would lose a maximum of 0.2% of workers per day. This corresponds to 0.2 g of ants per day or about 1.2 kcal. He determined that if a *P. rugosus* colony stops foraging during the peak foraging season, the ant colony would lose 12 g (61 kcal) of seed intake per day (MacKay 1982). In summary, a nest would lose more than 50 times more energy by stopping foraging activities than by continuing to forage under constant spider density. If ants were to continue foraging, however, then spider density would increase, leading to heavy ant mortality. If ants stopped foraging, spiders would migrate to active ant colonies. Since *P. rugosus* stores large quantities of seeds in their nests, it is feasible to forfeit aboveground activity. MacKay (1982) showed that after spiders left the area of the colony, ants became active again within 24 h. This behavior pattern resembles that of *M. wasmanni*. Hence, the cessation of foraging demonstrated in this study seems to be an effective, but time-consuming strategy to eliminate spiders from the immediate vicinity of nests. The period of time (hours/days) *Z. elegans* spiders spend at closed nest entrances under natural conditions and the cues that trigger the reopening of nest entrances are unknown.

Effect of predation on activities inside the nest

The perturbation experiments showed that events that directly affect workers engaged in one task outside the nest also alter the intensity of task performance per size class inside the nest. This result supports a flexible

task-allocation system that enables the colony to respond rapidly to changes in demand for particular tasks. What keeps exterior workers inside the nest? In an ant colony, a forager leaves the nest on a mission, to collect food. In *Pogonomyrmex barbatus* (Smith F., 1858), interaction rates with at least two types of workers influence a forager's activity: (1) interactions with patrollers, who leave the nest each morning before foragers; the return of the first patrollers apparently informs the other exterior workers, including foragers, that it is feasible to leave the nest that day; (2) other returning successful foragers; and (3) interactions that a forager has later on (Gordon 1986). For instance, an encounter with an alarmed ant can change the forager's mission and send it back to the nest (Gordon 1986). This also seems to be true for *M. wasmanni* harvester ants. Moreover, it was not possible for patrollers to leave the nest because the entrances were closed. Furthermore, Gordon (1999, 2010) reported two ways in which workers adjust their behavior. First, from one h to the next, a worker may switch from one task to another. Second, a worker may change its active/inactive status, becoming inactive when it was active before, or vice versa. Such changes at the individual level adjust the task allocation of the colony, altering the number of ants engaged in the colony's tasks (Gordon 1999, 2010). Additionally, Gordon (1986, 1987) showed that experimental perturbations that directly affect the performance of only one task also indirectly affect the performance of other tasks. Accordingly, manipulations that increased the need for one task led to task switching by some workers and to fewer ants performing certain other exterior tasks (Gordon 1989). In the present study, predation pressure interfered not only with outside activities such as patrolling, foraging or midden work, but also with activities inside the nest by causing changes in the relative frequency of activities and slight changes in the daily activity pattern. The proportion of inactive workers significantly decreased in all size classes in response to nest closure. Furthermore, the number of food-processing minor- and major-workers decreased as well. In contrast, the proportion of workers performing self-groom, allo-groom and trophallaxis increased significantly. These results underline that different tasks are not independent. Instead, the behavior of one group of workers influenced the behavior of another. After nest closure, the significantly increased numbers of workers performing the above activities could reflect the previously active workers outside the nest. Moreover, workers can fill more than one role in a colony: a forager might forage for food at one moment and nurse larvae the next (Oster & Wilson 1978). This would explain the significantly increased relative frequency of trophallaxis, self- and allo-grooming when entrances were closed. Grooming behavior has different individual and collective functions such as the removal of deleterious microorganisms and parasites from the tegument (Jaccoud *et al.* 1999; Hughes *et al.* 2002). Furthermore, their collective function is related to the maintenance of colony odor homeostasis (Lenoir *et al.* 1999).

Marked foragers

Only a small proportion of the marked *M. wasmanni* foragers switched to food processing, while the majority was inactive, grooming or patrolling the interior of the nest. Inside the nest, marked foragers performed tasks such as brood care or nest maintenance. These results indicate that, similar to *P. barbatus*, *M. wasmanni* workers might switch tasks in one direction, but not in others. In *P. barbatus*, the general pattern of task switching is a flow of workers into foraging (Gordon 1986). The flow seems to originate with young workers from inside the nest that previously performed brood care or food storage. Subsequently, when these young workers grow older, they switch to nest maintenance – a transition between interior and exterior activities. Importantly, once an ant switches from nest maintenance work to another exterior activity, it will not switch back. Therefore, new nest maintenance workers are recruited from younger workers inside the nest (Gordon 1986). Evidence for this form of behavioral flexibility remains limited for *M. wasmanni*.

Conclusions

This study showed that the activity pattern and behavior of the Mediterranean harvester ant *M. wasmanni* were modified not only by microclimatic conditions, but also by biological factors (the presence of predators exerted a considerable influence). *Messor wasmanni* colonies responded to predation by the obligate myrmecophagous spider *Z. elegans* in two ways: 1) they attacked the invader, and 2) they stopped foraging and closed nest entrances. Importantly, the laboratory experiments showed that the capture of only a single worker ant triggers nest closure at the end of aboveground foraging activity 100%. Thereafter, entrances could remain closed for six days. This usually causes *Z. elegans* individuals to leave the area of inactive

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colonies and move to active nests nearby. The present results also indicate that activities outside and inside the nest are interdependent: the numbers of workers engaged in one task depend on the number of workers engaged in another. As colony needs change, e.g., closed nest entrances in response to predation pressure, the numbers of workers engaged in each task are adjusted. Workers switch from one task to another, although not every type of transition is possible. Only a small proportion of marked *M. wasmanni* foragers switched to food processing, whereas the majority was inactive, grooming or patrolling the interior of the nest. Further research is required on how individual workers change tasks, and how colonies change the allocation of effort to different tasks in response to environmental changes such as predation pressure.

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7. Discussion

The results comprise eight years of studies and research about the Mediterranean harvester ant *M. wasmanni* on the Croatian island Cres as well as under laboratory conditions. The harvester ant *M. wasmanni* is the most abundant harvester ant species on the island. Another harvester ant species which occurs in markedly lower frequency is *Messor capitatus* (Latreille, 1798).

The results of the two original research papers and the manuscript, which constitute this doctorate thesis, cover research on several aspects of the biology of *M. wasmanni* harvester ants. The aim was to investigate (i) the native food spectrum, (ii) size-matching, (iii) harvesting efficiency as well as (iv) the behavioral responses of *M. wasmanni* harvester ant colonies to the predation by the obligate myrmecophagous spider *Z. elegans*. In the following, the core findings will be recapitulated and set in context to each other.

7.1. Morphology (Paper I, II)

Because ant size can vary in the various colonies and in the different distribution areas, the ant morphology (head width between the eyes [mm]) was measured in the course of this doctoral thesis. *M. wasmanni* workers are weakly polymorphic and show slight allometry with continuous size variation (Traxler 2016b). These results are in accordance with a preliminary investigation about the presence of allometric growth of workers in *M. wasmanni* and *Messor minor* (André, 1883) colonies occurring in Italy (Solida *et al.* 2007).

7.2. Description of the nest (Manuscript I)

Similar to the nest architecture of *M. pergandei* Mayr, 1886, (Wheeler & Rissing 1975) the typical nest of a *M. wasmanni* colony is underground and generally has one to two openings at ground level by which the ants enter and leave the nest. These openings are clearly visible. As displayed in **Figure 7b**, the nest surfaces are cleared of vegetation. *M. wasmanni* workers defoliate plants which grow too close to the nest (**Figure 7b**) (Rissing 1988). The mean diameter of cleared *M. wasmanni* nest surfaces was 71.9 ± 16.0 cm (mean \pm SD, N = 35), while the mean distance between nest entrances and chaff piles was 22.2 ± 12.0 cm (mean \pm SD, N = 35). Furthermore, a chaff pile, mainly comprising the husks of seeds, forms a semicircle at the outer edge of the nest surface (**Manuscript I**).

The clearing of the nest surface has provoked a number of hypotheses. On one hand, this clearing could remove the anchors for the spider webs (Schmidt 2016) such as web-building spiders. They are believed to be a major reason why species in the genus *Pogonomyrmex* clear all vegetation from the nest surface and from foraging trails (MacKay 1982; Schmidt 2016). On the other hand, Wu 1990 summarized that these open areas could also function as dehumidifier or heat absorber. Another proposed theory is that plants would provide unwelcome shade for the nest and they would compete for soil moisture and that associated roots would destroy the nest architecture, such as nest tunnels and

chambers. Furthermore, vegetation-free areas function as a target for flying males from other nests seeking mates. Or, the open area makes it easier for foraging workers to move about quickly (Wu 1990).

a)



b)



Figure 7 a) Defoliated *Marrubium vulgare* L. plants in close vicinity to a *M. wasmanni* nest. **4 b)** A *M. wasmanni* nest surface that is cleared of vegetation. All photographs by T. Traxler.

The excavation of a colony has shown that just below the nest entrances there are large chambers called “granaries”, partly filled with chaff and seeds (**Figure 8**). Farther down seed-storage granaries and finally rooms containing mixtures of larvae and pupae were found (unpublished data).



Figure 8 Granaries directly below the soil surface are partly filled with seed and chaff.
Photograph by T. Traxler.

7.3. Foraging and the native food spectrum (Paper I)

“Harvester ant” is a common name for any of the species or genera of ants, which consume seeds (granivory) (Bach 2013). Gathering seeds is usually performed by collecting plant propagules or larger plant parts (Steinberger *et al.* 1991). Seed storage is apparently common to harvester ants of the genus *Messor* (Hölldobler & Wilson 1990) and *Pogonomyrmex* (MacKay & MacKay 1984). *M. wasmanni* harvester ants store vast quantities of seeds in granaries within the nest (still unpublished data) to overcome times of scant seed availability in spring or due to inactivity outside the nest in response to predation (Azcárate *et al.* 2005). When predation becomes moderate, ant colonies are able to simply stop foraging and even close nest entrances with pebbles (**Paper II**).

During field observations for **paper I** of this doctoral thesis it could be observed that *M. wasmanni* colonies are forming narrow trunk trails, typically dendritic in form. These trunk trails reached total lengths up to 26.7m and connect nest entrances with foraging areas (Traxler 2016a). At the outer edge of the nest surface, trunk trails originated as a single pathway, then splitted into branches and finally into twings where workers disperse singly and forage for food (**Figure 9**). Workers cleared these pathways from vegetation in order to allow large numbers of ants to travel easily (Traxler 2016a).

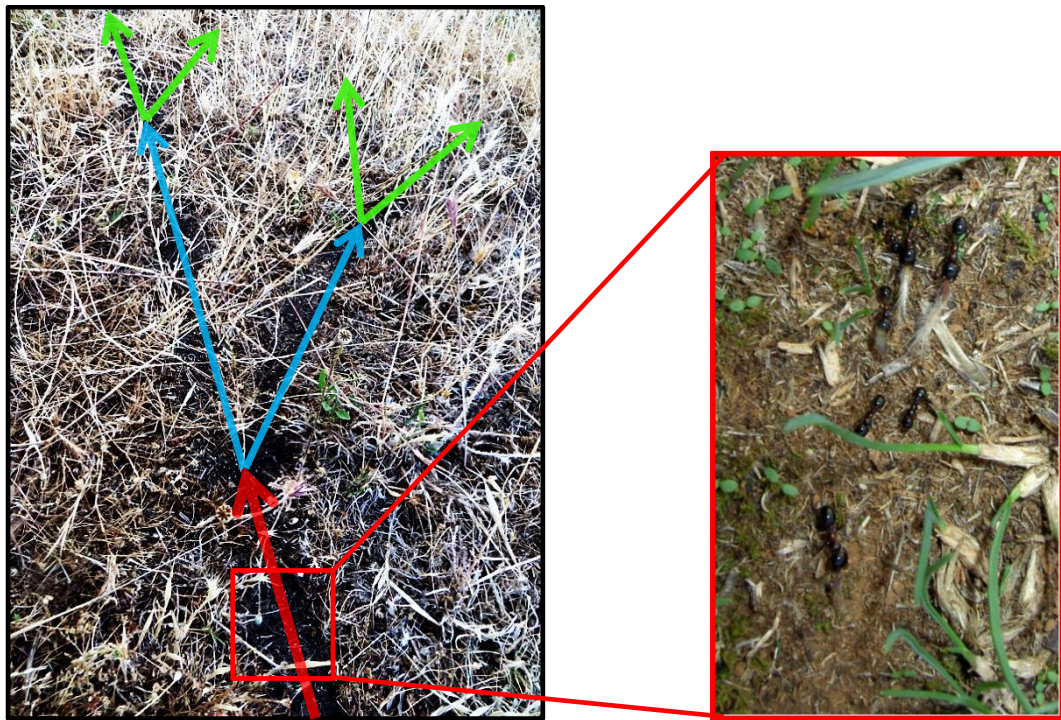


Figure 9 A trunk trail system of *M. wasmanni* which splits into branches and finally into twigs. Countless workers move back and forth on a daily basis. Photograph by T. Traxler.

Foraging activities showed a seasonal pattern where the highest activity levels occurred during spring and much lower foraging activities were observed in summer and autumn (**Figure 2** in **Paper I**) (Traxler 2016a). Furthermore, results show that the distributional pattern of the main food resources of *M. wasmanni* colonies changed constantly during sampling seasons (spring, summer and autumn). Based on these findings, the following conclusions can be drawn: 1. main food plants occur in different regions of the foraging area. 2. some plant species grow in distinct small regions, while others are distributed over large areas of the foraging ground. Consequently, foraging strategies are a mixture of individual foraging and column foraging, which are adjusted to the daily needs of an ant colony (Hölldobler & Wilson 1990, Traxler 2016a). Such foraging pattern is obviously displayed by species of *Messor* and *Pogonomyrmex* (Hölldobler & Wilson 1990) and meets following requirements: a) in order to discover newly-produced seed sources, which are separated from each other, workers (patrollers) continuously need to explore the different areas of the foraging area; b) for the exploitation of rich seed sources, which are concentrated in distinct areas, ants possess a recruiting system by which large numbers of workers are guided by means of recruitment pheromones exactly to these accumulated food items (column foraging) (Hölldobler & Wilson 1990, Traxler 2016a). Furthermore, foraging *M. wasmanni* workers picked up seeds from the ground (post-dispersal seed predation) or plucked them right off the plant (pre-dispersal seed predation). Moreover, different plant parts, such as parts of leaves, stems, petals, parts of infrutescences like

capsule walls and awns were frequently collected and later rejected, presumably not serving as food (Traxler 2016a). This observation is in accordance to findings by Hensen (2002) and Waser (1998) on harvester ants *Messor bouvieri* Bondroit, 1918, *M. pergandei* and *M. timidus* Espadaler, 1997.

Granivore harvester ants of the genus *Messor* prey on seeds (Hahn & Maschwitz 1985, Hobbs 1985, Reyes-López & Fernández-Haeger 2002), but results show that they subsist on much more than that. Although *M. wasmanni* harvester ants primarily prey on seeds, they occasionally consume arthropods and gastropods as well. A survey of the composition of their food spectrum was made by taking samples from loaded foragers returning to the nest on three days per sampling season in May 2009, July/August 2009 and October 2009. Approximately 3.700 objects could be identified and categorized in three different groups:

1. Seeds, fruits and vegetative plant parts such as leaves, stems, parts of flowers other than seeds and fruits;
2. Parts of arthropods or whole arthropods, orthoptera-faeces, sheep-faeces, snail shells and living gastropods;
3. Small stones and clods of soil.

Plant material represented the vast majority (max. 97.5%) of harvested material in all sampled seasons (**Figure 2 in Paper I**). Regarding gathered animal remains, some authors claim (Brown *et al.* 1979, Baroni-Urbani 1987) that granivorous ants prefer dead insects to seeds. *M. barbarus* Linnaeus, 1767 workers for example can react with intense recruitment and foraging activity to unusual protein food sources (Lopez *et al.* 1992). This claim has not been observed in *M. wasmanni* workers. They only occasionally (max. 2.6% of the collected propagules) gathered animal remains. But nonetheless the analysis of collected food items as well as the analysis of chaff piles (**Paper I, Manuscript I**) showed that *M. wasmanni* colonies consume a wide variety of arthropods, land snails, as well as maritime gastropoda. Gastropoda and coleoptera seem to be preferred by *M. wasmanni* harvester ants. While analyzing the chaff pile material, 43 animal taxa have been identified. Gastropoda dominated with a relative frequency of 53%, including 26 taxa. Coleoptera were found with a relative frequency of 38%, which represents the second most common animal group found in chaff piles (**Manuscript I**). The largest values of gathered animal remains (2.6%) were found in May 2009, compared to merely 0.6% in July/August 2009 and 0.7% in October 2009 (Traxler 2016a). It is assumed that these collected animal remains represent a complementary protein source (Azcárate *et al.* 2005) in the diet of *M. wasmanni* colonies, especially when the seed and fruit availability is scarce in spring and during periods of drought (Azcárate *et al.* 2005). Moreover, the sporadic collection of clods of soil can be explained by the presence of resin exudates on them (Fernández-Escudero & Tinaut 1993).

7.3.1. Size-matching and harvesting efficiency (Paper I)

In this study it is hypothesized that the polymorphic worker caste of *M. wasmanni* harvester ants optimize food collection by delegating the task of carrying larger loads to larger workers and smaller loads to smaller workers (size-matching). Results suggest that under natural conditions *M. wasmanni* workers do not conduct size-matching at foraging trails (**Figure 10-11**). Little, if any, variance in size of loads selected can be attributed to body size of foragers (Traxler 2016a).

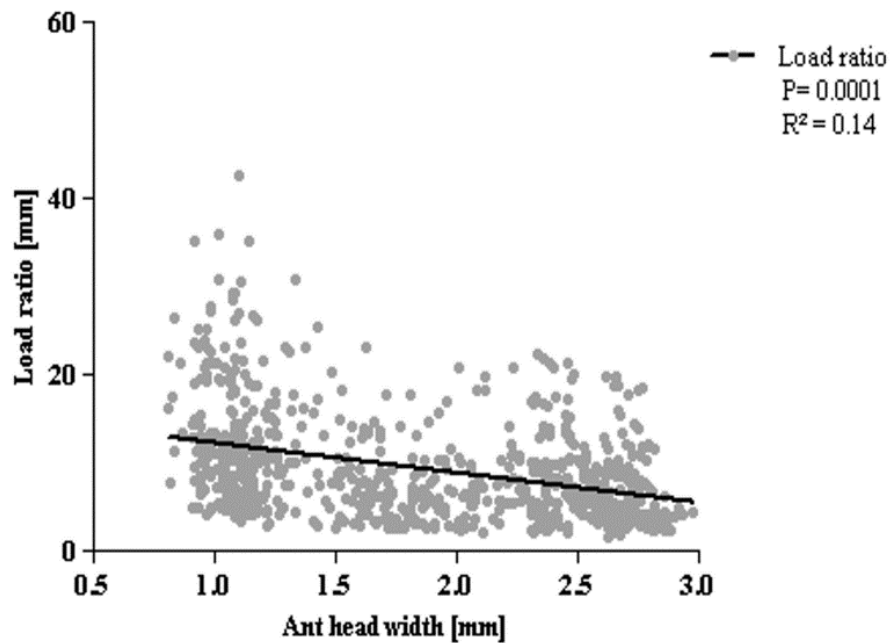


Figure 10 In the scatter diagram the correlation between load ratio and ant size is shown. The load ratio was calculated as follows: (ant size [head width] + load size)/ant size. The data shows random samples of returning foragers of a single *M. wasmanni* colony (N = 776). One dot represents one observation. Linear regression analysis revealed a low negative correlation between ant size and load ratio. The larger the worker size class, the smaller the range in the load ratio. Residuals from regressions were approximately normally distributed around zero in all cases (Traxler 2016a).

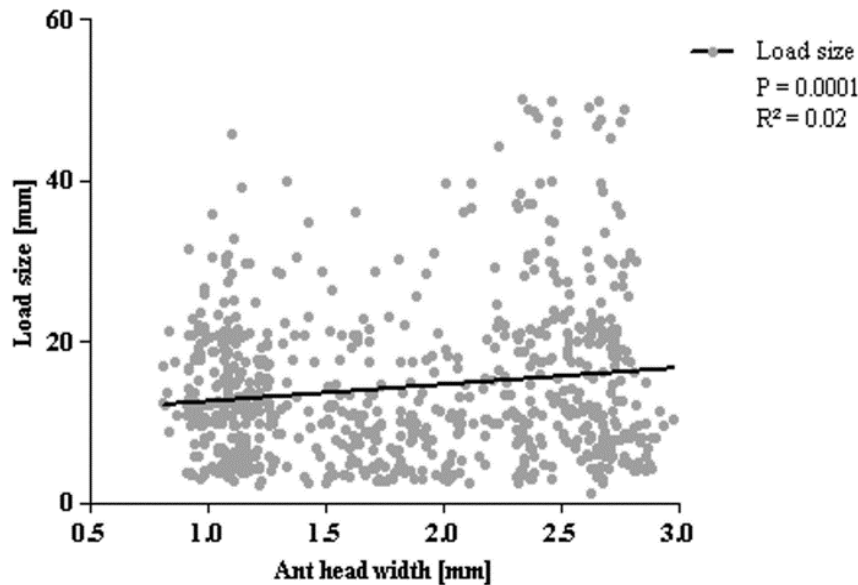


Figure 11 In the scatter diagram the correlation between load size and ant size is shown. The data shows random samples of returning foragers of a single *M. wasmanni* colony (N = 776). One dot represents one observation. Linear regression analysis revealed a very low positive correlation between ant size and load size, indicating only a small tendency for major-sized workers to carry larger loads than minor-sized workers. Residuals from regressions were approximately normally distributed around zero in all cases (Traxler 2016a).

Although a linear regression analysis revealed a significant negative correlation between worker ant head width and load ratio and a positive correlation between worker ant head width and load size, the low to extremely low R^2 values explained only 2.8-14.9% of the variance in the size of loads. Additionally, small-sized workers did not appear to be constrained by load size. Only a slight tendency for minor-sized workers compared to major-sized workers to carry smaller loads (in relation to their body size) was found. The small extent of size-matching in *M. wasmanni* harvester ants suggests that the individual performance of workers may be an inadequate measure of colony foraging success. The parameter of load mass is probably a more meaningful parameter than the parameter of load size.

7.3.2. Harvesting efficiency (Paper I)

Foraging activity of harvester ant colonies is closely related to food availability (Detrain *et al.* 2000). Hence, harvesting efficiency of *M. wasmanni* colonies varied strongly from May to October 2009. Results revealed that, on high frequented foraging trails, foragers brought not only greater quantities of food items to the nests, but also the proportion of laden ants over the total number of incoming foragers per size class increased as a function of the colony activity (Traxler 2016a). Furthermore, harvesting efficiency varied between size

classes. While the harvesting efficiency of media- and major-sized workers decreased considerably from May to October 2009, the opposite trend was observed for minor-sized workers. Because worker size classes are not equally endowed against heat shock risks, the sensitivity to high temperatures is expected to decrease with worker size and cuticle thickness (Heredia & Detrain 2005). This may explain the large number of minor-sized workers present along foraging trails in October 2009 and the increased harvesting efficiency at this season. The decreasing harvesting efficiency of major-sized workers from May to October 2009 may reflect the specialization of this size class on the performance of other tasks, such as cutting plant leaves, patrolling for favoured food sources (Gordon 2002), or defending functions as highlighted in *M. barbarus* (Detrain & Pasteels 2000). Results show that *M. wasmanni* major-sized workers are also effective fighters against predators, such as ant-eating zodariid Thorell, 1881 spiders, which are very abundant in close proximity to ant colonies and foraging trails throughout the summer (Traxler 2016b).

7.3.3. Speed related to soil surface temperature (Paper I)

Although *M. wasmanni* workers differ in size, body size does not significantly influence the speed of burdened ($R = 0.027$, $p = 0.743$, $N = 153$) and unburdened ants ($R = 0.015$, $p = 0.859$, $N = 153$). The speed of either loaded or unloaded *M. wasmanni* workers is significantly dependent upon soil surface temperature (**Table 3**). Nonetheless, the relationship of burdened major-sized workers to soil surface temperature was minor with only 0.8% of the explained variance ($R^2 = 0.08$, $p < 0.001$). This value increases to 15.0% for unburdened major-sized workers ($R^2 = 0.15$, $p < 0.0001$). In both analyses, the dependent variable was worker speed and the independent variable was surface temperature. Similar relationships have been detected in *M. barbarus* (Azcárate *et al.* 2007), *M. capitatus* (Nielsen & Baroni-Urbani 1990), *M. pergandei* (Rissing 1982) and *Pogonomyrmex* spp. (Morehead & Feener 1998).

Table 3 Worker speed (cm/s) as a function of soil surface temperature (°C) assessed by linear regression analysis. The dependent variable was worker speed and the independent variable was soil surface temperature. R² value specifies how much of the total variation in the dependent variable can be explained by the independent variable. F-test shows if there is a linear relationship between the two variables (in other words, the null hypothesis is R² = 0). Larger beta values are related with lower p-values and larger t-values. The t-statistics and the two-tailed p-values are utilized in testing whether a given coefficient is significantly different from zero. N - number of samples; df - degrees of freedom; p - the statistical significance of the regression model; B - values predict the dependent variable from the independent variable; Std. error - the standard errors associated with the coefficients; Beta - standardized coefficients; t - t-statistics; p - two-tailed p-values (Traxler 2016b).

Variable	ANOVA					Unstandardized coefficients		Standardized coefficients		
	N	R ²	df	F	p	B	Std. error	Beta	t	p
Minor-sized unloaded	226	0.26	1	79.14	<0.0001	-0.27	0.03	-0.51	-8.90	<0.0001
Minor-sized loaded	275	0.23	1	82.70	<0.0001	-0.23	0.03	-0.48	-9.09	<0.0001
Media-sized unloaded	505	0.20	1	123.71	<0.001	-0.19	0.02	-0.44	-11.12	<0.0001
Media-sized loaded	476	0.32	1	218.52	<0.001	-0.32	0.02	-0.56	-14.78	<0.0001
Major-sized unloaded	208	0.15	1	35.83	<0.0001	-0.14	0.02	-0.39	-5.99	<0.0001
Major-sized loaded	146	0.08	1	12.53	<0.001	-0.13	0.04	-0.28	-3.54	<0.001

7.4. Chaff piles (Manuscript I)

A Central European *Messor*-colony collects approximately 27.000 seeds per day, mainly cereal grains. Accordingly, ants collected an estimated total of 12 kg seeds during a four-month harvesting period (Veile 1991). In contrast, the analysis of the chaff pile material of the Mediterranean harvester ant *M. wasmanni* revealed a wide spectrum of plant species. **Table 4** shows that the average fresh weight of chaff pile material per nest ranged from 771.5 g in the north (Merag, Loznati) of the distribution area of *M. wasmanni* colonies on the island of Cres to 1008.0 g in the southern area (Osor, Punta Križa).

Table 4 Comparison of dry weight of chaff pile material collected in the north (Merag, Loznati), middle (Zaglav, Belej) and south (Osor, Punta Križa) of the distribution zone of *M. wasmanni* on the island of Cres.

Sampling site	N	Minimum (g)	Maximum (g)	Mean (g)	SD
North	11	405.0	1120.0	771.5	234.8
Middle	10	475.0	1284.0	802.2	256.5
South	11	529.0	1987.0	1008.0	461.3

Plant material, including seeds, fruits and other plant parts, found in chaff piles made up 90.88% and comprised 55 plant species of 21 plant families. The Jaccard Index revealed a similarity of approximately one third between plant species found in chaff pile samples collected in the north, in the middle and in the south of the distribution area of *M. wasmanni* colonies on the island of Cres. Moreover, results showed that although seeds from 55 plant species are on the menu, only some species have favored status (**Table 5**). In chaff piles, only two eudominant and four dominant plant species were found. In a physically demanding environment in which *M. wasmanni* harvester ants occur, only a few plant species produce a profitable crop of seeds during any given year to live on. This interpretation of the ecological meaning of a broad spectrum of food plants is supported by a study on *Messor structor* (Latreille, 1798) (Hahn & Maschwitz 1985).

Table 5 Recovery rate in percent of food plants which occurred in chaff piles of *M. wasmanni* colonies. Light grey: eudominant and dominant plant species, dark grey: plant species that occurred in chaff piles in each of the three sampling sites; N = chaff piles collected in the north (Merag, Loznati) of the distribution area of *M. wasmanni* colonies on the island of Cres; M = chaff piles collected in the middle (Zaglav, Belej) and S = chaff piles collected in the south (Osor, Punta Križa) of the distribution area of *M. wasmanni* colonies at Cres. 1 = eudominant, 2 = dominant, 3 = subdominant, 4 = recedent, 5 = subrecedent, 6 = sporadic.

Family	Species	Type of diaspore	N		M		S	
			%	Dominance-class	%	Dominance-class	%	Dominance-class
Apiaceae	<i>Daucus carota</i> L.	Schizocarpic fruit	0.35	5	0.00	-	0.00	-
Apiaceae	<i>Foeniculum vulgare</i> Mill.	Schizocarpic fruit	0.00	-	0.23	6	0.00	-
Apiaceae	<i>Tordylium apulum</i> L.	Achene	4.45	3	0.00	-	0.06	6
Asteraceae	<i>Carduus pycnocephalus</i> L.	Achene	0.00	-	0.00	-	0.38	6
Asteraceae	<i>Carthamus lanatus</i> L.	Achene	1.31	4	2.06	4	5.22	3
Asteraceae	<i>Crepis dioscoridis</i> L.	Flower head	0.47	5	0.01	6	0.00	-
Asteraceae	<i>Scolymus hispanicus</i> L.	Achene	1.38	4	0.00	-	0.00	-
Asteraceae	<i>Crepis verrucosa</i> Gaertn.	Merica	0.00	-	0.00	-	14.49	2
Asteraceae	<i>Crepis verrucosa</i> Gaertn.	Flower head	0.71	5	0.00	-	0.26	6
Boraginaceae	<i>Echium plantagineum</i> L.	Nutlet	0.11	6	7.30	3	0.00	-
Brassicaceae	<i>Capsella rubella</i> Reut.	Half of pods	0.74	5	0.00	-	0.00	-
Caryophyllaceae	<i>Petrothagia saxifraga</i> L.	Capsule	0.59	5	0.00	-	0.00	-
Caryophyllaceae	<i>Silene vulgaris</i> Garcke	Capsule	0.00	-	0.01	6	0.00	-

Cichoriaceae	<i>Urospermum picroides</i> L.	Achene	3.31	3	0.00	-	0.02	6
Cistaceae	<i>Helianthemum</i> sp.	Capsule	0.04	6	0.00	-	0.86	5
Convolvulaceae	<i>Convolvulus althaeoides</i> L.	Seed	0.88	5	22.51	2	0.00	-
Euphorbiaceae	<i>Euphorbia wulfenii</i> Hoppe	Seed	0.30	6	0.06	6	0.05	6
Fabaceae	<i>Anthyllis vulneraria</i> L.	Pod	1.10	4	0.00	-	0.00	-
Fabaceae	<i>Anthyllis vulneraria</i> L.	Calyx	1.01	4	0.00	-	0.00	-
Fabaceae	<i>Astragalus hamosus</i> L.	Pod	0.12	6	0.00	-	0.00	-
Fabaceae	<i>Lotus corniculatus</i> L.	Pod	0.01	6	0.00	-	1.25	4
Fabaceae	<i>Medicago arabica</i> L.	Pod	0.93	5	0.00	-	0.44	5
Fabaceae	<i>Medicago carstiensis</i> L.	Pod	0.00	-	0.07	6	0.07	6
Fabaceae	<i>Medicago rigidula</i> (L.) All.	Pod	0.27	6	0.05	6	0.00	-
Fabaceae	<i>Medicago minima</i> L.	Pod	6.55	3	58.09	1	2.24	4
Fabaceae	<i>Medicago orbicularis</i> L.	Pod	0.03	6	0.02	6	0.00	-
Fabaceae	<i>Scorpiurus muricatus</i> L.	Mericaip	0.00	-	0.18	6	7.35	3
Fabaceae	<i>Trifolium campestre</i> Schreb.	Petal	0.50	5	0.00	-	30.88	2
Fabaceae	<i>Trifolium scabrum</i> L.	Calyx	5.61	3	1.44	4	11.11	2
Fabaceae	<i>Trifolium angustifolium</i> L.	Calyx	0.64	5	1.34	4	0.00	-
Fabaceae	<i>Trifolium stellatum</i> L.	Calyx	0.17	6	0.00	-	0.00	-
Fabaceae	<i>Trigonella balansae</i> Boiss & Reut	Pod	2.54	4	0.00	-	3.84	3
Fabaceae	<i>Trigonella balansae</i> Boiss & Reut	Flower+Calyx	0.00	-	0.00	-	0.35	5
Geraniaceae	<i>Erodium cicutarium</i> L.	Mericaip	47.85	1	0.00	-	0.00	-
Geraniaceae	<i>Erodium cicutarium</i> L.	Awn	3.61	3	0.00	-	0.00	-
Lamiaceae	<i>Marrubium vulgare</i> L.	Calyx	0.96	5	0.00	-	0.00	-
Lamiaceae	<i>Marrubium vulgare</i> L.	Leaf	0.22	6	0.00	-	0.00	-
Lamiaceae	<i>Salvia officinalis</i> L.	Mericaip	0.51	5	0.00	-	0.00	-

Lamiaceae	<i>Salvia verbenacea</i> L.	Calyx	0.00	-	0.00	-	0.20	6
Lamiaceae	<i>Thymus vulgaris</i> L.	Calyx	0.00	-	0.00	-	0.59	5
Linaceae	<i>Linum austriacum</i> L.	Capsule	0.00	-	0.00	-	0.07	6
Linaceae	<i>Linum austriacum</i> L.	Calyx	0.62	5	0.00	-	0.00	-
Malvaceae	<i>Malva sylvestris</i> L.	Schizocarpic fruit	0.01	6	0.00	-	0.00	-
Plantaginaceae	<i>Plantago lanceolata</i> L.	Capsule	0.00	-	0.42	5	5.53	3
Plantaginaceae	<i>Plantago lanceolata</i> L.	Spike	0.00	-	0.18	6	1.15	4
Poaceae	<i>Aegilops neglecta</i> Req.	Spikelet	3.06	4	5.32	3	1.16	4
Poaceae	<i>Aegilops triuncialis</i> L.	Spikelet	0.17	6	0.00	-	0.00	-
Poaceae	<i>Anthoxanthum odoratum</i> L.	Spikelet	0.00	-	0.00	-	1.64	4
Poaceae	<i>Anthoxanthum odoratum</i> L.	Husk	0.00	-	0.00	-	0.95	5
Poaceae	<i>Avena sterilis</i> L.	Spikelet	3.19	3	0.14	6	0.37	5
Poaceae	<i>Avena sterilis</i> L.	Awn	0.04	6	0.00	-	0.00	-
Poaceae	<i>Anisantha sterilis</i> L.	Husk	0.60	5	0.00	-	0.00	-
Poaceae	<i>Cynodon dactylon</i> Pers.	Spike (parts)	0.00	-	0.00	-	0.75	5
Poaceae	<i>Cynosurus echinatus</i> L.	Spikelet	0.70	5	0.26	6	0.00	-
Poaceae	<i>Dasyphyrum villosum</i> (L.) Borbás	Spikelet	0.00	-	0.00	-	5.99	3
Poaceae	<i>Catapodium rigidum</i> Hubb.	Stem	0.20	6	0.00	-	0.00	-
Poaceae	<i>Hordeum murinum</i> L.	Husk	1.14	4	0.00	-	0.00	-
Poaceae	<i>Melica ciliata</i> L.	Spikelet	0.32	5	0.21	6	0.00	-
Poaceae	<i>Poaceae</i> sp.	Husk	1.97	4	0.00	-	0.00	-
Poaceae	<i>Stipa</i> sp.	Awn	0.01	6	0.00	-	0.00	-
Poaceae	<i>Vulpia ciliata</i> Dumort.	Spikelet	0.34	5	0.00	-	0.00	-
Polygonaceae	<i>Rumex obtusifolius</i> L.	Fruit	0.15	6	0.00	-	0.00	-
Primulaceae	<i>Anagallis arvensis</i> L.	Capsule	0.05	6	0.00	-	2.41	4
Rubiaceae	<i>Sherardia arvensis</i> L.	Calyx	0.17	6	0.05	6	0.34	5
Rubiaceae	<i>Sherardia arvensis</i> L.	Mericaip	0.01	6	0.00	-	0.00	-

Rubiaceae	<i>Sherardia arvensis</i> L.	Calyx	6	0.05	6	0.34	5
Rubiaceae	<i>Sherardia arvensis</i> L.	Mericaip	6	0.00	-	0.00	-

Furthermore, in chaff piles of *M. wasmanni* colonies 21 types of dispersal units (diaspores) and other plant parts were identified. Chaff pile material was chiefly composed of schizocarpic fruits with a share of 34%, followed by pods (17.2%), Petals (9.5%), Calyxes (9.2%), spikelets (7.9%) and seeds (7.5%) (**Figure 12**). These results are in accordance with the granivorous diet of ant species of the genus *Pheidole*, *Monomorium* Mayr, 1855, *Pogonomyrmex* and *Messor* (Andersen 1991).

Results show that granivory is a general trend of the *M. wasmanni* harvester ant species, which coincides with numerous observations for this genus (Hahn & Maschwitz 1985, Cerdá & Retana 1994, Detrain & Pasteels 2000, Azcárate *et al.* 2005). Granivorous harvester ants collect seeds and other diaspores, which are stored in the nest in communal chambers called granaries. Subsequently, collected diaspores are threshed and separated from less palatable parts. Finally, seeds are stored in specific granaries for further consumption. The chaff will be ejected from the nest and accumulates in piles near the entrance at the nest surface (Hölldobler & Wilson 1990, Veile 1991). In addition, results show that *M. wasmanni* harvester ants are not too choosy about seeds and other dispersal units. When most favored seeds and diaspores become scarce, *M. wasmanni* harvester ants may turn to less desirable seeds and non-seed plant material such as petals, flower parts, calyxes, leaves and stems. This finding is in accordance with the result of the study on the harvester ant *Veromessor pergandei* (Mayr, 1886) (Rissing & Wheeler 1976). Moreover, larger quantities of germinable seeds were found in chaff piles (**Figure 12**). Resulting, *M. wasmanni* harvester ants may play an important role in the dynamics of plant communities by both acting as seed dispersal agents and as seed predators (Hölldobler & Wilson 1990). Granivore harvester ants such as *M. wasmanni* are distinguished from the even broader group of ant species, such as *Formica rufa* Linnaeus, 1761 that collect seeds only because of elaiosomes, which are nutritious appendages, shaped like caps or sheaths, attached on the seeds. Foragers discard seeds as soon as they have taken off these elaiosomes, anywhere between the plant and the nest (Ridley 1930). Resulting, these ant species are major dispersers of myrmecochorous plants. In contrast, harvester ants feed on the seeds themselves (granivory). Yet results show their effect on the plants they visit is not wholly negative. They also disperse plants because from time to time they lose seeds along their foraging trails or they discard seeds by accident on the chaff piles. In this way, they compensate in part the damage caused by seed predation (Hölldobler & Wilson 1990).

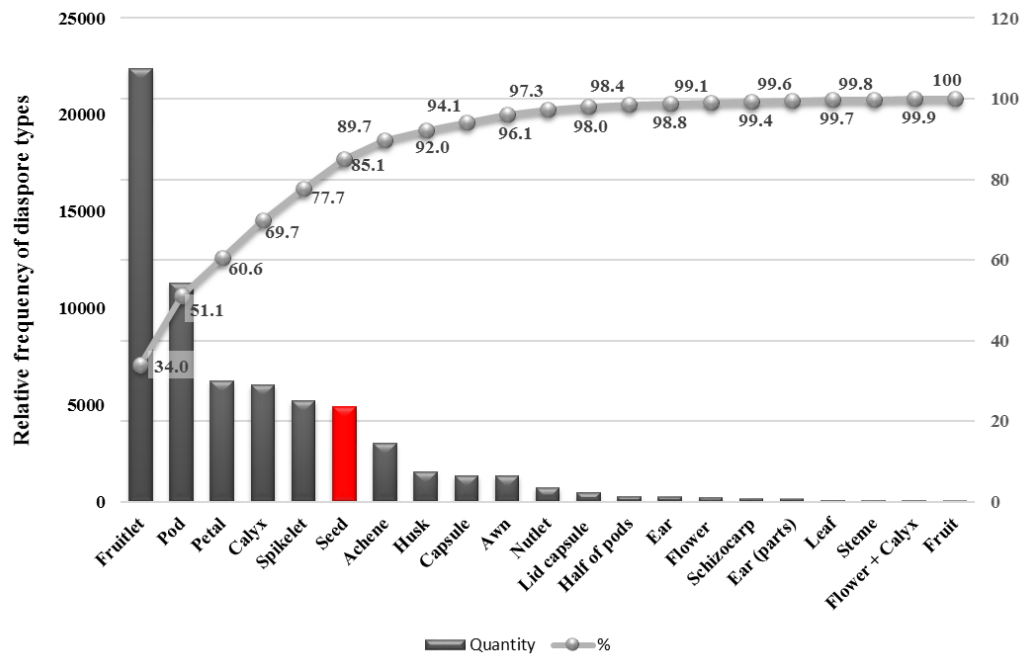


Figure 12 Relative frequency of diaspore types in chaff piles of *M. wasmanni* colonies (Manuscript I).

7.5. Predation by myrmecophagous spiders (Paper II)

Numerous reported studies deal with search behavior, prey switching, and handling time in predator species (e.g. Pekár & Křál 2002, Pekár 2004, Pekár *et al.* 2005, Pekár 2009, Pekár & Toft 2014), less attention is paid to behavior of the prey species.

Some cases have been described in which ant species adjust their nests in response to parasites or predators. For example, Colonies of *Formica subsericea* Say, 1836 close their nest entrances with materials such as pebbles, soil, or grass after being raided by the slave-making ant *Formica subintegra* Wheeler, 1908. Furthermore, they remove the traces of excavated soil and discarded cocoons that otherwise characteristically litter the nest surface (Talbot & Kennedy 1940). Another ant species, *Myrmecocystus mimicus* Wheeler, 1908, plugs nest entrances and covers the surrounding area with sand in response to raids from neighboring colonies of the same species (Hölldobler 1981). A similar phenomenon has also been reported for harvester ants of the genus *Pogonomyrmex* and *Cataglyphis* Foerster, 1850. Workers of the harvester ant *Pogonomyrmex rugosus* Emery, 1895 respond to persistent predation by the western window spider (*Latrodectus Hesperus* Chamberlin & Ivie, 1935) by closing nest entrances and decreasing or even halting their foraging activities, even when less than 0.2 percent of the population is predated per day (MacKay 1982). A similar behavior has been described in the Florida harvester ant *Pogonomyrmex badius* (Latreille, 1802), which is harassed by the theridiid spider *Steatoda fulva* (Keyserling, 1884) (Hölldobler 1971a).

7.5.1. Spider attack and nest closure (Paper II)

There are few predator-prey systems which are sufficiently simple to test the general idea of nest closure in response to predation. However, the ant-eating spider *Z. elegans* and the Mediterranean harvester ant *M. wasmanni* are such a system.

Results show that immediately after being bitten by a *Z. elegans* spider, the *M. wasmanni* worker ant became excited and moved around with opened mandibles and attacked both the surrounding area and the spider, which generally quickly fled to a safe distance. In the meantime, nest mates that passed by and antennated the attacked ant. As a consequence, they became excited too and started moving around with opened mandibles (Traxler 2016b). Following a spider bite, the bitten ant started to stumble, its movements gradually decreased, and the gaster bent under the mesosoma. This described C-shaped body posture lasted for several minutes, after which the whole body became paralyzed. The mean paralysis latency was 16.64 ± 7.82 (N = 6). Frequently (83.3%, N = 5), within 3.62 ± 4.76 min (mean \pm SD; N = 5) after the attack, spiders approached from their retreat, stretched out their forelegs and palpated their prey. If the prey was still defensive, spiders retreated again (Traxler 2016b).

Results presented in **Paper II** showed that activity patterns of *M. wasmanni* harvester ant colonies were not only modified by microclimatic conditions (Azcárate *et al.* 2007, Cole *et al.* 2010, Ruano *et al.* 2000) but also by predation (Traxler 2016b). Predation by zodariid ant-eating spiders exerts considerable influence on the activity pattern of the concerning *M. wasmanni* harvester ant colonies. They responded to predation in two ways: 1) they attack and chase away the invader, and 2) they stop foraging and close nest entrances (**Figure 13**) (Traxler 2016b).



Figure 13 Closed nest entrances at the end of aboveground activity in response to predation. Photograph by T. Traxler.

Furthermore, perturbation experiments under laboratory conditions showed that the capture of only a single worker ant is sufficient to trigger nest closure with 100% confidence at the end of aboveground foraging activity. The nest entrances could remain closed for a maximum of six days. Consequently, under natural conditions, *Z. elegans* individuals usually leave the area of inactive colonies and move to active nests nearby (Traxler 2016b). These results correspond well with those found for American harvester ants *P. badius* (Gentry 1974) and *P. rugosus* (MacKay 1982), which ceased foraging for seven to ten days. MacKay (1982) calculated, if *P. rugosus* colonies would continue foraging and if spider density did not change, the nest would lose a maximum of 0.2% of workers per day, in other words 0.2 g of ants per day. MacKay (1982) estimated that if a *P. rugosus* colony were to stop foraging during the peak foraging season, the colonies would lose 12 grams (61 kcal) of seed intake per day. In summary, a *P. rugosus* harvester ant colony would lose more than 50 times more energy by stopping foraging activities, than by continuing to forage under constant spider density. But, if colonies were to continue foraging, the spider density would increase, leading to heavy ant mortality. If ants stopped foraging activity, spiders would migrate to active colonies. Since *P. rugosus* colonies store vast quantities of seeds in their nest, it is feasible to forfeit aboveground activity. Moreover, MacKay (1982) found that after spiders left the area of the colony, ants became active again within 24h. This pattern of behavior resembles that of *M. wasmanni* harvester ants (Traxler 2016b). Moreover, Gentry (1974) underlined, that through a decline in aboveground activity as a result of predation, the entire ant colony can be prevented from being destroyed. For predators, the effort needed for maintenance at an inactive colony or in the local area to take large numbers of foraging workers was too great and it would move on. This strategy takes the pressure off the ant colony and allow it to regain its strength through replacement of lost workers. Furthermore, harvester ants such as *M. wasmanni* and *Pogonomyrmex* sp. maintain seed reserves every year, what colonies allow to survive an extended period with few or no foragers or with closed entrances over a longer period (MacKay 1982). The following Chapter provides the results of performed studies about the predation by the ant-eating spider *Z. elegans* and its influence on activities inside the nest (**Paper II**).

7.5.2. Effect of predation on activities inside the nest (Paper II)

Under laboratory conditions, exterior workers made up approximately 24% of the total adult *M. wasmanni* colony, with interior workers being the remainder. The subsequent question in **paper II** was, whether perturbation outside the nest such as predation by ant-eating spiders would affect the number of ants performing tasks inside the nest as well. Previously, the relative frequency of activities inside the nest without predation pressure was determined. Perturbation experiments revealed that events which directly affect workers engaged in one task outside the nest also alter the intensity of task performance per size-class of workers inside the nest as well (Traxler 2016b). Results presented in this study

support a flexible task-allocation system, which enables the colony to respond rapidly to changes in the demand for particular tasks (Traxler 2016b).

What keeps exterior workers inside the nest? In an ant colony, a forager leaves the nest on a mission, to collect food. In *Pogonomyrmex barbatus* (Smith 1858) harvester ant colonies, interaction rates with at least two types of workers influence a forager's activity: first, interactions with patrollers, who always leave the nest before foragers; the return of the first patrollers to the nest apparently informs the other exterior workers, including foragers, that it is feasible to leave the nest that day; second, other returning successful foragers to the nest; and interactions that a forager has later on (Gordon 1986). For example, an encounter with an alarmed worker ant can change the forager's mission and send it back to the nest (Gordon 1986). This also seems to be true for *M. wasmanni* harvester ant colonies. Moreover, it was not possible for patrollers to leave the nest because of closed nest entrances. Results of the present study show that predation is not only interfered with outside activities such as patrolling, foraging or midden work, but also with activities inside the nest by causing changes in the relative frequency of activities. Additionally, these results show that *M. wasmanni* workers must be making moment-to-moment decisions about whether to perform their task actively or not (Traxler 2016b). According to Gordon (1999), *Pogonomyrmex* harvester ants adjust their behavior in two ways: 1) a worker may switch from one task to another from one hour to the next; 2) a worker may change its active/inactive status. These described changes at the individual level adjust the task allocation of the colony, altering the number of ants engaged in the colony's tasks (Gordon 1999).

Results revealed that the number of inactive workers significantly decreased in all size-classes in response to predation and nest closure. Several studies support the hypothesis that inactive workers form a pool of uncommitted reserves can start to work when they are stimulated by external conditions (Gordon 1989, Gordon 1999, Porter & Jorgensen 1981, Wilson 1983). Furthermore, the proportion of food-processing minor- and major-workers also decreased. In contrast, the number of workers performing self-groom, allo-groom and trophallaxis increased significantly (**Table 6**). These findings suggest that different tasks are not independent. Instead, the group of workers performing one task influenced the behavior of another group of workers. After the closure of nest entrances, the significantly increased numbers of workers performing the above mentioned activities could reflect the previously active workers outside the nest (Traxler 2016b). Furthermore, it was hypothesized that in a colony, workers can fill more than one role. According to Oster & Wilson (1978), a forager might forage for food at one moment and nurse larvae the next. This would explain the significantly increased relative frequency of self- and allo-grooming workers as well as workers performing trophallaxis, when entrances were closed (Traxler 2016b). The grooming behavior has diverse individual and collective functions in an ant colony such as the removal of deleterious microorganisms and parasites from the tegument (Jaccoud *et al.* 1999, Hughes *et al.* 2002). Additionally, Lenoir *et al.* (1999) pointed out that their collective function is related to the maintenance of colony odor homeostasis.

Table 6 The effect of spider predation on the number of ant workers performing specific activities inside the nest. Undisturbed conditions comprising 30 days of observation: N(minor) = 30,822, N(medium) = 7,464, N(major) = 2,302; disturbed conditions comprising nine days of observations: N(minor) = 7,950, N(medium) = 1,859, N(major) = 819. The average per day was calculated. The analysis examines if there is a difference in the number of workers performing one activity under undisturbed conditions and under disturbance (predation pressure). A Wilcoxon matched-pairs signed rank test was used as non-parametric test because data were assumed to be not normally distributed. W: sum of signed ranks. p: the p value is used as an indicator whether the difference between the mean of two groups is likely to be due to chance. *: $p = 0.01 - 0.05$, **: $p = 0.001 - 0.01$, ***: $p \leq 0.001$ (Traxler 2016b).

Activity	Minor-workers		Medium-workers		Major-workers	
	W	p	W	p	W	p
Inactivity	72.00	**0.0024	78.00	***0.0005	62.00	*0.0122
Patrolling	0.00	1.0000	36.00	0.1763	3.00	0.9219
Nest maintenance	-26.00	*0.0313	-13.00	0.1250	20.00	0.1829
Carrying food	2.00	0.9527	35.00	0.0829	1.00	1.0000
Food processing	52.00	*0.0425	40.00	0.0830	46.00	*0.0452
Trophallaxis	-74.00	**0.0015	-78.00	***0.0005	43.00	*0.0273
Self-groom	-76.00	***0.0010	-68.00	**0.0049	-68.00	**0.0086
Allo-groom	-72.00	**0.0024	-58.00	*0.0112	-39.00	*0.0195
Brood care	-26.00	0.3394	-38.00	0.1514	-34.00	0.1475

7.5.3. Marked foragers (Paper II)

Results show that only a small proportion of the marked *M. wasmanni* foragers switched to food processing, while the majority was inactive, grooming or patrolling the interior of the nest. In contrast, any of the marked foragers was observed performing tasks such as brood care or nest maintenance (**Figure 14**). Results further indicate that *M. wasmanni* workers might switch tasks in one direction, but not in others (Traxler 2016b). Similar to the harvester ant *P. barbatus*, the general pattern of task switching could be a flow of workers

into foraging (Gordon 1986). Yet, evidence for this form of behavioral flexibility remains limited for *M. wasmanni* harvester ant colonies.

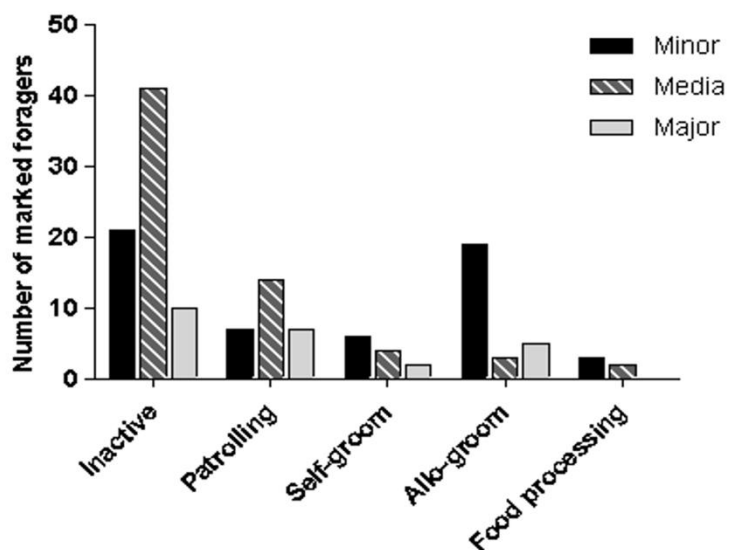


Figure 14 Tasks performed by marked foragers inside the nest when nest entrances were closed due to predation pressure. The number of workers per activity was summarized during the duration of three perturbation experiments. 30 workers, i.e. 10 Minor-sized workers, 10 Medium-sized workers and 10 Major-sized workers, were marked for the experiment (Traxler 2016b).

8. Conclusion

M. wasmanni is a harvester ant species, which typically builds narrow and dendritically formed trunk trails (**Paper I**). These pathways are usually cleaned from vegetation in order to allow large numbers of ants to travel easily (Hölldobler & Wilson 1990). In the same manner nest surfaces are cleared, however, the advantage of this is still unclear (**Manuscript I**).

In chaff piles, plant material accounts for 90.88% of the total quantity and comprised 55 plant species of 20 families. Merely two eudominant and four dominant plant species were found. The Jaccard Index revealed a similarity of approximately one third between plant species compositions found in chaff pile samples collected in the north, in the middle and in the south of the distribution area of *M. wasmanni* colonies on the island of Cres. This composition is characteristic for the physically demanding environments, with only few plant species possessing a profitable crop of seeds during vegetation periods, in which *M. wasmanni* harvester ants occur. In this context Rissing & Wheeler (1976) also stated that when most favored seeds and diaspores become scarce harvester ants may turn to less desirable seeds and non-seed plant material such as petals, flower parts, calyxes, leaves and stems. Regarding this, chaff pile material comprised a total of 21 types of dispersal units and other plant parts. This results indicates that *M. wasmanni* harvester ants are not particularly choosy about the types of collected propagules and dispersal units. Chaff pile material was chiefly composed of schizocarpic fruits with a share of 34%, followed by pods (17.2%), Petals (9.5%), Calyxes (9.2%), spikelets (7.9%) and seeds (7.5%) (**Manuscript I**). When most favored seeds and diaspores become scarce, *M. wasmanni* harvester ants may turn to less desirable non-seed plant material such as petals, flower parts, calyxes, leaves and stems. Moreover, as results show, larger quantities of germinable seeds were found in chaff piles. Resulting, *M. wasmanni* harvester ants play an important role in the dynamics of plant communities by both acting as seed predators and as seed dispersal agents (Hölldobler & Wilson 1990). The ants disperse plants along their foraging trails by losing dispersal units or they accidentally deposit the diaspores at the chaff piles. In this way, the damage caused by seed predation is partly compensated (Hölldobler & Wilson 1990).

The name “harvester” wrongly implies a strict vegetarian diet, however, although *M. wasmanni* harvester ants primarily prey on seeds, they occasionally consume animal remains, such as arthropods and snails. Analysis of the chaff piles and collected propagules revealed a variety of arthropod fragments, land snails and marine gastropods (**Paper I, Manuscript I**). A total of 43 animal taxa were found in the chaff pile material, where gastropoda made up the main part with 53%, followed by coleoptera with 38% (**Manuscript I**). The highest proportions of animal remains were found in May 2009 (2.6%) followed by July/August 2009 (0.6%) and October 2009 (0.7%) (Traxler 2016a). These collected animal remains presumably provide a complementary protein source (Azcárate *et al.* 2005) in the diet of *M. wasmanni* colonies, especially when the seed and fruit availability is scarce in spring and during periods of drought (Azcárate *et al.* 2005).

Study results further imply that under natural conditions *M. wasmanni* workers do not conduct size-matching along foraging trails (**Paper I**). Little, if any, difference in size of selected propagules (e.g. seeds, other diaspores and plant parts) could be related to the body size of foragers. The low to extremely low R^2 values (2.8-14.9%) indicate that size-matching in *M. wasmanni* is biologically and practically not significant, although it was found to be statistically significant (Traxler 2016a). This indicates that individual performance may be an inadequate measure of colony foraging success for *M. wasmanni*. Other sources of variability such as individual metabolism due to varying worker size (Nielsen & Baroni-Urbani 1990) may play a more important role in the specific harvesting efficiency (Cerdá & Retana 1994). Moreover, it was found that slight allometry with continuous size variation leads to different harvesting efficiency in *M. wasmanni* harvester ants. The harvesting efficiency of minor-sized increased considerably from May to October (Traxler 2016a). The sensitivity to high temperatures is presumably increased with small worker size and low cuticle thickness (Heredia & Detrain 2005). This may be an explanation of the increased harvesting efficiency of minor workers in October 2009.

Furthermore, this study showed that the activity pattern and behavior of *M. wasmanni* were not only modified by microclimatic conditions but also by biological factors, such as predation by ant-eating spiders (**Paper II**). *M. wasmanni* colonies responded to predation by the obligate myrmecophagous spider *Zodarion elegans* in two ways: 1) medium- and major-sized workers attacked the predator, and 2) foraging was stopped and nest entrances were closed. Additional observations under laboratory conditions confirmed that the capture of only one worker ant is sufficient to trigger the nest closure at the end of aboveground foraging activity with 100% confidence. The resulting closure of nest entrances remained up to six days (Traxler 2016b). As a consequence, under natural conditions, *Z. elegans* individuals usually leave the area of inactive colonies and move to active nests nearby.

The present results also indicate that activities outside and inside the nest are interdependent. As the colony experienced a change, e.g. closed nest entrances in response to predation, the tasks of engaged workers were adjusted. Workers can switch from one task to another, however, not every type of transition is possible. Observations of marked foragers showed, that only a small proportion of ants switched to food processing, while the majority was inactive, groomed or patrolled inside the nest. None of the marked foragers was observed performing tasks such as brood care or nest maintenance (Traxler 2016b).

Further studies are required to investigate how individual workers change tasks and how colonies change the allocation of different tasks in response to environmental impacts, such as predation.

9. References

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