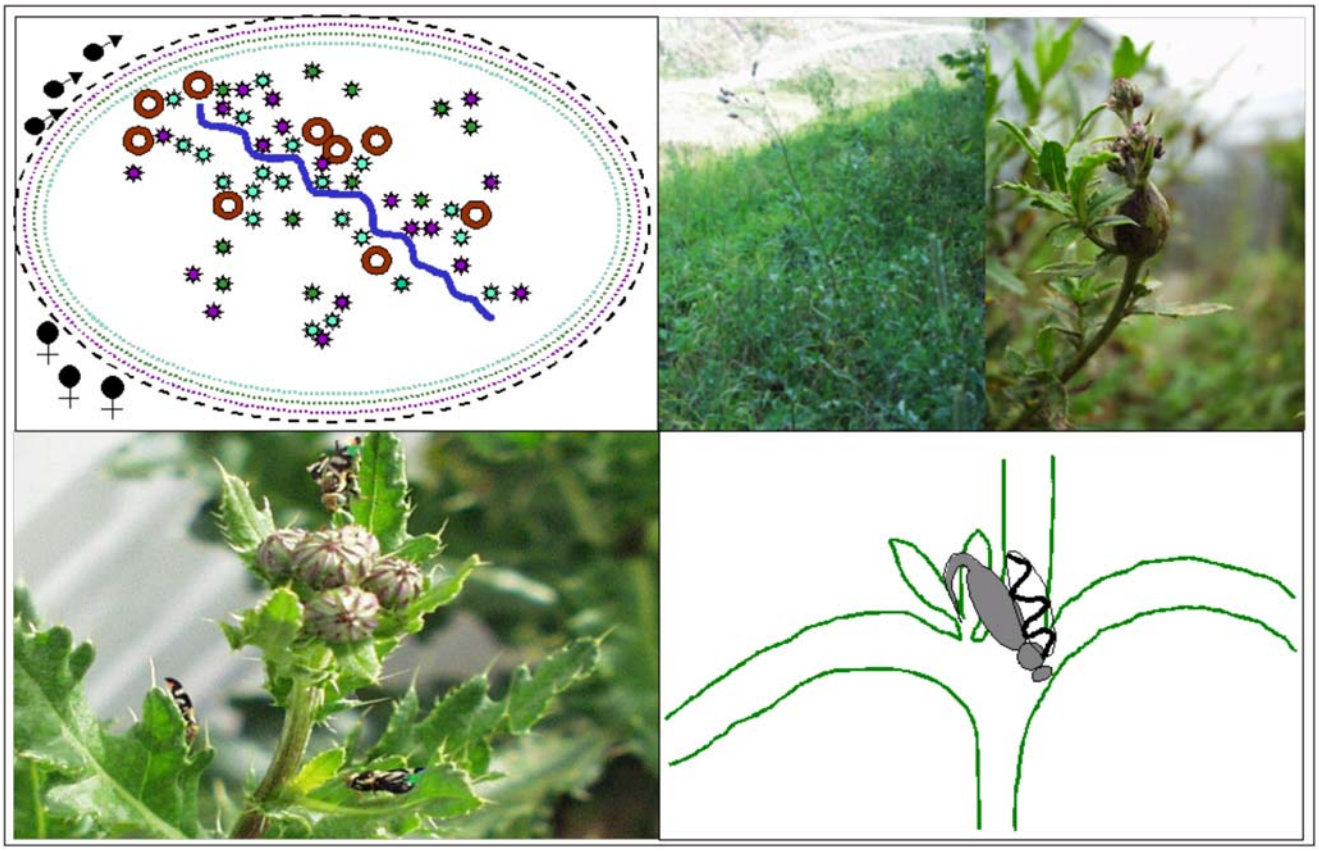
The complex foraging strategy of the specialised gall fly *Urophora cardui* (Diptera: Tephritidae) for host plants (*Cirsium arvense*, Asteraceae)

Wiltrud Daniels



The complex foraging strategy of the specialised gall fly *Urophora cardui* (Diptera: Tephritidae) for host plants (*Cirsium arvense*, Asteraceae)

Dissertation

zur Erlangung des Grades eines
Doktors der Naturwissenschaften
Dr. rer. nat. –
der Fakultät Biologie/Chemie/Geowissenschaften
der Universität Bayreuth

Vorgelegt von

Wiltrud Daniels

Bayreuth, Mai 2004

1 Introduction

W. Daniels

Department of Plant Physiology, NWI, 95440 Bayreuth, wiltrud.daniels@uni-bayreuth.de

The great majority of all animals on earth interact with plants in their effort to survive and reproduce (Schoonhoven, 1990). For herbivorous insects, interactions with plants are of critical importance, since plants are not only used as a food source but also as a place for mating and egg-deposition (Feeny, 1975; Price *et al.*, 1980; Schoonhoven, 1990; Schoonhoven & Jermy 1998). In turn, plants are subject to selection forced upon them through usage by the insects (Schoonhoven & Jermy, 1998). Other influences, for example human usage, climate, fire or grazing by macro-herbivores also pose selection-pressures on the first trophic level, but herbivorous insects remain the most abundant group, measured either by species abundance or individual abundance (Schoonhoven, 1990).

Since they set the initial conditions for nearly all the following processes in the microhabitat, mating and oviposition are the key behavioural patterns performed by herbivorous insects (Dettner *et al.,* 1997b; Price, 1992; Schoonhoven & Jermy, 1998; Strong *et al.,* 1984; Zwölfer, 1994). Mating is not only a prerequisite of the reproductive success of the individuals involved, it also has the consequence of facilitating evolution (Headrick & Goeden, 1994; Jiggins & Bridle, 2004). In many herbivorous insects oviposition is closely linked to mating (Papaj, 1994; Raghu *et al.*, 2002). Both behaviours also play an important role on population dynamics (Preszler & Price, 1988; Price *et al.*, 1990). If the functions of mating and oviposition of herbivorous insects in terrestrial ecosystems are considered in this ecological background they also have an influence on population dynamics of other species (Masters & Brown, 1997).

For a better comprehension of the biology of one species, including its population structure, it is necessary to conduct a careful analysis of all interactions with other species (Cornell & Lawton, 1992; Tscharntke, 1992). Such a food web analysis helps unravel evolutionary processes (Dettner *et al.*, 1997; Price, 1992; Zwölfer & Arnold-Rinehart, 1993). Furthermore, such analyses provide a useful tool in the search for general patterns of population dynamics (Price *et al.*, 1995). With the growing concern for the environment in the last years the study of food webs has become also politically important (Harris, 1991).

Investigation of mating and oviposition combines several major theoretical areas in evolutionary ecology and is thus an exciting and rewarding area of research (Charnov & Skinner, 1985): these include game theory (Parker & Smith, 1990), life history theory (Fritz *et al.*, 2003) and foraging theory (Pyke, 1984). Recently chemical ecology has become important in regard to mating and oviposition, too (Dutton *et al.*, 2000). Behavioural plasticity is also of importance (Casiraghi *et al.*, 2001) as are the morphology of the ovipositor and the antennae (Vilhelmsen *et al.*, 2001). On the one hand structural constraints of both organs limit the host plant range of the insect (Fletcher & Prokopy, 1991), although on the other hand the morphology and sensitivity of the receptors on the ovipositor and the antennae are

improved by adaptive selection, which enhances reproductive fitness by improving the host plant recognition ability of the insect (Altner & Prillinger, 1980; Brown & Anderson, 1998).

The complex behaviour of host plant selection by herbivorous insects will now be described in more detail. In the course of host plant choice, the quality of the plant should be crucial for the female (Burkhardt & Zwölfer, 2002; Hassell & Southwood, 1978; Mappes & Kaitala, 1995), since higher quality ensures a higher larval survival (Baylis & Pierce, 1991). Often host plant quality is associated with the nitrogen supply of the plant (Fox *et al.*, 1990; Stamp & Bowers, 1990), but other aspects, like water supply can also affect quality for a certain insect species (Horner & Abrahamson, 1992; Preszler & Price, 1988; Ramløv & Lee, 2000; Waring & Price, 1988). High host plant quality does not necessarily imply that the host plant performs well (de Bruyn, 1995; Scheirs & de Bruyn, 2002). Not only host quality directly, but more basically the quality of the host's habitat is important, since it may influence host density and additionally host quality (Diaz-Fleischer & Aluja, 2003). This interface between the host plant and its abiotic growing conditions can act as an evolutionary force on the insect's dispersal strategies (Holt & Lawton, 1993; Simberloff & Stiling, 1996), host plant selection strategies and population density (Price, 1992). Thus the effects of the abiotic environment via the larval host play a central role for the herbivorous insect in determining time and space of population densities and performance (Price, 1992).

A further feature, which often has a significant impact on herbivorous insects, is the influence of natural enemies, respectively predators and parasitoids, the latter being often more important (Bernays, 1990). For an analysis of the selection for a suitable host plant in herbivorous insects it is not only important to include the third or the first trophic level, but to take also interactions between all three levels into account (Achtziger, 1997; Micha *et al.*, 2000; Shiojiri & Takabayashi, 2003). Plant density and the size of plant stands will affect the herbivore and its predators and parasitoids alike (Price *et al.*, 1980). Plant density has also indirect effects on the performance of the larvae of a particular herbivore and its associated parasitoid and predator species, since plant density influences the microclimate (Feeny, 1970; Price, 1988), nutritional quality (Scriber & Slansky, 1981; Stamp & Bowers, 1990), the concentration of certain nutrients in the plant tissue, and the presence of secondary plant volatiles (Cornell, 1983; Evans, 1990; Monaco *et al.*, 1982; Schoonhoven, 1972). The latter are considered to attract parasitoids especially in order to control the herbivore (Bouletreau, 1986; Dutton *et al.*, 2000). However secondary plant volatiles also can be used as signals by the herbivorous insect (Bäckmann *et al.*, 2001; Ignacimuthu *et al.*, 2000; Müller & Hilker, 2000; Turlings *et al.*, 1990).

Several years ago it was quite popular to discuss the role of top-down (exerted by parasitoids or predators) and bottom-up (generated by resource availability) effects in terrestrial ecosystems (for example Power, 1992; Scheirs & de Bruyn, 2002) and the topic is still controversial. In complex systems with at least three trophic levels, it is difficult to assess the influence of one of these forces. The presence and quality of host plants is often as important (for example Baylis & Pierce, 1991; Obermaier & Zwölfer, 1999; Stamp & Bowers, 1990) as protection from natural enemies (for example Ballabeni *et al.*, 2001; Berdegue *et al.*, 1996; Lill *et al.*, 2002) or density-dependent dispersal of the phytophagous insect (for example Dempster *et al.*, 1995; Freese, 1995; Zwölfer & Völkl, 1997). These effects may interact with each other (Biere *et al.*, 2002), they may change each others importance or be similarly important (Hunter & Price, 1992).

Because these complex systems are difficult to study, smaller models such as self-contained small eco-systems like plant galls (Angermann, 1986) of herbivorous insects (Mani, 1964) are used: these are where the larvae develop (Bronner, 1992; Mani, 1992). Since the larvae are not able to leave their host plant, accurate host plant selection by the female becomes crucial (Ballabeni *et al.*, 2001), since the larvae are not able to compensate for a non-adaptive choice performed by their mother. In this case the behaviour of the female sets the initial conditions from which any larval interaction may proceed (Mayhew, 1997). The evolution of these gall structures is described as an example of unilateral exploitation of the morphogenetic capacities of the plant, since in this case it is not beneficial for the plant (Allee *et al.,* 1967). This is one of the reasons, why gall insects are often used in biological control of weeds (Harris, 1989; Harris & Shorthouse, 1996; Peschken *et al.*, 1982; Redfern & Cameron, 1989; Zwölfer, 1968).

Nowadays studies that can be related to biological control (Harris, 1991) of weed or pest species have become important once more (Baars *et al.*, 2003; Denoth *et al.*, 2002; Jiggins & Bridle, 2004; Kruess, 2002). After the first enthusiasm about having found a non-chemical, cheap and highly successful method of weed and pest control, several critical arguments about general practice in biological control have been raised (Baars *et al.*, 2003; Denoth *et al.*, 2002). It therefore becomes necessary to study the causes of indirect effects, in order to avoid deleterious effects in future release projects and to understand their mechanisms. If host-specific biocontrol agents establish in a new habitat, but are not able to reduce their hosts' density, indirect effects can link the target weed to other native organisms and thereby expand the impacts of the invasive weed (Pearson & Callaway, 2003). Today we have a worldwide situation of introduced exotic species, acting as biocontrol agents, outnumbering exotic weed species for which they were introduced (Denoth *et al.*, 2002). Extensive studies of the host plant selection behaviour of galling insects before their integration in control projects is therefore of a critical importance (Harris, 1989; Harris & Zwölfer, 1968; Harris, 1991)

Host plant selection is one of the most complex behavioural sequences in insects. It involves different defined steps, which have to follow each other in a sequence. In the literature many different classifications of these steps can be found, depending on the study system (Fletcher & Prokopy, 1991; Mangel & Roitberg, 1993; Mangel & Roitberg, 1989; Nagelkerke, 1994; Rosenheim & Mangel, 1994). The number of these steps also vary according to the study system (Mangel & Roitberg, 1989; Roitberg, 1990; Rosenheim & Mangel, 1994). From step to step, detection and selection of a suitable larval host become more finely tuned (Zwölfer, 1968).

The first task of the female is to select a certain habitat and a special searching strategy is needed in order to detect host plant stands (Nordlund, 1994; Weis & Kapelinski, 1984; Whitham, 1978). The searching strategy includes features of time allocation to a single host plant stand; it determines how many patches a female will try to visit and how many eggs are deposited in each stand (Nagelkerke, 1994; Roitberg, 1990). Once in a host plant stand, the female has to select the plant that seems most suitable for larval development (Bernays & Chapman 1994; Mayhew, 1997; West & Cunningham, 2002). After arriving on this selected plant, the female still has to find a particular plant organ that is suitable for oviposition (Chun & Schoonhoven, 1973; Dutton *et al.*, 2000; Hattori, 1988; Lynn & Chang, 1990). Afterwards, the clutch size has to be adjusted to the host plant quality (Godfray, 1987; Lalonde &

Roitberg, 1994). In Hymenoptera the female additionally faces the question of the sex ratio to produce (Craig *et al.*, 1992; Fox *et al.*, 1990).

In the course of the present study host plant recognition and selection was studied in the specialised gall fly *Urophora cardui* on its host plant *Cirsium arvense. U. cardui* is one of the two only *Urophora* species, which induces galls not in the thistle head but in the stem (the other species is *U. misakiana* on *C. setidens* in East Asia (H. Zwölfer pers. comm.)). Nearly all sister taxa occur on Carduae. Gall formation is obviously a derived character (Zwölfer & Arnold-Rinehart, 1993). The ancestor was presumably achene mining (Zwölfer & Rinehart, 1994; Zwölfer & Arnold-Rinehart, 1993). The gall, which is induced by *U. cardui,* is the most derived in the genus. Gall structure enables the larvae to recruit nutrients from the whole host plant, not only the galled side shoot (Lalonde & Shorthouse, 1985). Thus the study species is of evolutionary interest. Additionally the larvae are highly dependent on host plant fitness, which implies that an optimal choice by the females is necessary, which makes *U. cardui* a suitable object for the study of foraging strategies.

C. arvense is an aggressive weed species, not only in Europe, but also in the northern USA and Canada, where it has been accidentally introduced. *U. cardui,* as one of its specialised herbivores, was established as a biocontrol agent in the 1970s (Peschken & Harris, 1975). The release of *U. cardui* as a biological control agent provides preliminary information about its host plant selection process, especially in relation to habitat characteristics (Peschken & Derby, 1997; Peschken *et al.*, 1982; Peschken & Harris, 1975; Shorthouse & Lalonde, 1986): it became obvious that host plant usage is low compared to other species (Goeden, 1987), which is presumably related to its complex and rigid selection behaviour.

After a description of important life history factors and the biology of the study system the following nine questions are posed:

1) What are the main characteristics of foraging behaviour in *U. cardui*?
2) How rigid is the host plant template of *U. cardui* exhibited in different choice situations?
3) How do males and females of *U. cardui* select for a suitable host plant stand?
4) Which factors determine the time until a decision for a particular host plant is derived?
5) Which host plant cues are important for the selection by females of *U. cardui*?
6) Which senses are used by males and females for host plant recognition and selection?
7) Is there any impact of the substance the males use for territory marking?
8) What is the ultrastructure of the ovipositor like, which receptors can be found on it and what implications can be derived for the selection process of a particular host plant organ?
9) Which host plant cues are used by the females to select a certain host plant organ as oviposition site?

After the particular chapters, which cover these different questions, a model of the host plant selection process by *U. cardui* is discussed. This is followed by the synopsis.

10 Summary

Nearly all herbivorous insects in terrestrial ecosystems depend on plants for their survival and reproduction. Additionally they dominate all terrestrial ecosystems due to species and individual abundance. Interactions between these two groups are thus of a high significance for the analysis and the understanding of the complex interactions in terrestrial ecosystems. Especially foraging for host plants by herbivorous insects is of a central importance.

In the present thesis the foraging strategy of the specialised gall fly *Urophora cardui* on the creeping thistle, *Cirsium arvense,* was investigated as a model system for the foraging process of a specialised herbivorous insect.

Males and females of *U. cardui* use the larval host plant as their rendezvous place. The males establish territories on the plant, which they defend against conspecific males. The females lay eggs into axillary buds, in order to initiate gall development.

- Male and female body size, measured as weight at eclosure or capsule width, was not correlated with male respectively female longevity. Generally males lived shorter than females. Capsule width of males and females was not significantly different, while weight at eclosure and fresh weight at death was. Females weighed more, which may be due to their higher need of energy during adult life. Both sexes lost body weight during life, at their death there was still a significant difference between the sexes, but it was less prominent than at eclosion.
- All behaviours, which are performed by males and females on their host plant were defined, recorded and analysed. The females spent most of the time they were on a plant on resting, probing axillary buds, running on the plant and grooming. The males spent most of the time they are on a particular plant on copulation and patrolling their territory. The behaviour of both sexes was highly variable between individuals. Concerning the movement pattern on an already chosen host plant, the females concentrate on the upper parts of the host plant. They were mainly occupied with an extensive probing of various axillary buds, which occurred with a higher probability in a suitable developmental stage at the top of the plant. In contrast the males patrolled the whole plant, although only the upper leaves became marked. If they encountered another male on their territorial plant threatening and fighting were inevitable. Fights lasted several hours interrupted by threatening periods. Mating of males and females usually followed oviposition.
- Neither females nor males accepted modified host plants or models of thistles. Their behaviour on modified thistles was reduced mainly to running around the plant and grooming, if they stayed long enough to enable observation. These results indicate a rigid host plant template using the input of several senses, thus the flies always recognise models and modified plants as a non-host plant.
- Both sexes were able to discriminate host plants and non-host plants from a distance of 0.8-2m. They decided for a particular plant already from this distance and flew immediately to the selected one, before they really entered the host plant stand.

- The time male and female flies needed until they selected one of the host plants in a particular host plant stand depended on the number of non-host plants, host plants and the number of suitable hosts. The decision-time became shorter, if there were not too many suitable host plants. This may be due to decreasing sampling time of the host plants present.
- *U. cardui* females did not prefer plants of a certain height. In contrast the branching level, which indicates the number of axillary buds, and the number of flower buds played a significant role during foraging for host plants. Plants with an intermediate branching level were preferred, while those with many flower buds, indicating a higher age, were avoided.
- The males of *U. cardui* were able to select their territorial plant on olfactory cues or on visual cues likewise. In contrast, the females were not able to recognise their host plant on olfactorial cues alone. But, if male-marked and unmarked host plants were available they significantly preferred the marked thistles. The differentiation between marked and unmarked *C. arvense* were made according to olfactorial cues, since the plants did not differ in their height, nor in their branching level, nor in the number of flower buds. Thus, female selection of larval host plants depended on male choice for territories. This result is remarkable, especially in evolutionary terms, since the males select the larval host for the offspring of their predecessor. Interestingly the males preferred plants marked by conspecifics also.
- On the tip of the females' ovipositor there is a receptor field with several morphological different receptor types. Mainly they seem to have mechanoreceptive as well as chemosensory functions. According to studies on other insect species they may also be able to analyse the water-content of the tissue. These receptors enable the females to measure and analyse the inner structure of the plant tissue at the axillary bud.
- The width of the apical meristem of the axillary buds was proven to influence female choice of the plant organ, where eggs become deposited. Axillary buds with an apical meristem-diameter above 0.62mm had a higher probability to became chosen by the *U. cardui* females. The clutch size was adjusted to the diameter of the apical meristem, indicating, that the females were able to estimate the quality of the respective axillary bud, which influences larval performance.

These results were summarized in a general model of the foraging strategy of *U. cardui*, as an example for other specialised herbivorous insects.

11 Zusammenfassung (German Summary)

Herbivore Insekten sind elementar von Pflanzen abhängig, nicht nur in ihrem Bestreben zu leben sondern auch in der Fortpflanzung. Als arten- und individuenreichste Gruppen in terrestrischen Ökosystemen stellen Pflanzen und Insekten die wichtigsten Gruppen dar. Interaktionen zwischen diesen beiden Gruppen sind deshalb von enormer Bedeutung für das Verständnis der komplexen Vorgänge innerhalb eines solchen Systems. Insbesondere der Wirtswahl herbivorer Insekten kommt hier eine zentrale Rolle zu.

In der vorliegenden Arbeit wurde die „foraging-strategy“ der spezialisierten Gallfliege *Urophora cardui* an der Ackerkratzdistel, *Cirsium arvense,* als ein Modellsystem für die Wirtswahl eines spezialisierten herbivoren Insektes, untersucht.

Die Männchen und Weibchen benutzen die Wirtspflanze der Larven als „Rendezvous“-Platz, wobei die Männchen an dieser Pflanze Territorien errichten, die sie gegen andere Männchen verteidigen. Die Weibchen legen Eier in die Knospen junger Seitentriebe. Dadurch wird die Bildung einer Pflanzengalle initiiert.

- Die Größe von Männchen und Weibchen, gemessen als Schlupfgewicht oder als Kopfkapselbreite, korrelierte nicht mit der Lebensdauer der Individuen. Männchen lebten generell kürzer als die Weibchen. Die Kopfkapselbreite der beiden Geschlechter unterschied sich nicht signifikant, während sowohl das Schlupfgewicht, als auch das Todesgewicht signifikant verschieden waren. Die Weibchen waren schwerer als die Männchen, was wahrscheinlich mit einem höheren Energiebedarf zusammenhängt. Individuen beider Geschlechter verloren im Laufe ihres Lebens an Gewicht, wobei die Differenz zwischen Männchen und Weibchen zum Todeszeitpunkt geringer als zum Schlupfzeitpunkt war.
- Alle Verhaltensweisen, die von Männchen und Weibchen an ihrer Wirtspflanze ausgeübt werden, wurden definiert, aufgenommen und analysiert. Die Weibchen verbrachten die meiste Zeit, die sie auf einer bestimmten Pflanze waren, damit zu ruhen, die Seitenknospen zu testen, die Pflanze zu belaufen, oder sich zu putzen. Die Männchen dagegen verbrachten die meiste Zeit, die sie sich auf ihrem Territorium befanden, damit zu kopulieren oder ihr Territorium zu patrouillieren. Das Verhalten beider Geschlechter war individuell sehr variabel. Was das Bewegungsmuster an sich betrifft, so befanden sich die Weibchen hauptsächlich am oberen Teil der Wirtspflanze, wo die Wahrscheinlichkeit, geeignete Seitenknospen zu finden, höher ist. Im Gegenteil dazu beliefen die Männchen die gesamte Wirtspflanze, wobei sie aber überwiegend die oberen Blätter mit dem Sekret ihrer Rektaldrüse markierten. Sobald sie auf ein anderes Männchen derselben Art trafen waren gegenseitiges Drohen und ein folgender Kampf unausweichlich. Derartige Kämpfe konnten bis zu mehrere Stunden in Anspruch nehmen. Die Paarung von Männchen und Weibchen erfolgte normalerweise nach der Eiablage durch die Weibchen.
- Weder die Männchen noch die Weibchen akzeptierten modifizierte Wirtspflanzen oder Distelmodelle. Ihr Verhalten auf modifizierten Wirtspflanzen war hauptsächlich auf das Belaufen der Pflanze sowie das Putzen reduziert, sofern

sie überhaupt lange genug auf der Pflanze blieben, um eine Beobachtung zu ermöglichen. Die Ergebnisse deuten auf ein sehr starres Wirtspflanzen - Suchbild sowie die Nutzung verschiedener sensorischer Modalitäten hin. Dadurch sind die Fliegen immer in der Lage, eine veränderte Pflanze oder ein Distelmodell als eine Nicht - Wirtspflanze zu erkennen.

- Beide Geschlechter konnten eine Wirtspflanze aus einer Entfernung von 0.8-2m erkennen. Sie entschieden sich für eine bestimmte Pflanze schon aus dieser Distanz, noch bevor sie einen Standort mit mehreren Wirtspflanzen richtig erreicht hatten.
- Die Zeit, die die Männchen und die Weibchen jeweils benötigten, bevor sie sich für eine bestimmte Pflanze an einem Standort entschieden, hing von der Anzahl der Nicht – Wirtspflanzen, der Zahl der Wirtspflanzen und der Zahl der geeigneten Wirtspflanzen ab. Die Entscheidungszeit wurde kürzer, wenn weniger geeignete Wirtspflanzen vorhanden waren. Dies ist wahrscheinlich auch darauf zurück zu führen, dass die Individuen weniger lange brauchten, um die vorhandenen Pflanzen zu evaluieren.
- Weibchen von *U. cardui* bevorzugten keine bestimmte Höhe ihrer Wirtspflanze. Der Verzweigungsgrad, der die Anzahl der Seitenknospen anzeigt, sowie die Anzahl von Blütenknospen spielten jedoch eine wichtige Rolle bei der Auswahl. Pflanzen mit einem mittleren Verzweigungsgrad wurden signifikant bevorzugt, während solche mit vielen Blütenknospen, die ein höheres Alter der Pflanze anzeigen, abgelehnt wurden.
- Männchen von *U. cardui* waren in der Lage, ihr Territorium entweder anhand von olfaktorischen oder anhand von visuellen Signalen auszuwählen. Im Gegensatz dazu waren die Weibchen nicht in der Lage ihre Wirtspflanze anhand des olfaktorischen Profils zu erkennen. Aber wenn sowohl von Männchen markierte Pflanzen wie auch unmarkierte zur Wahl gestellt wurden, so bevorzugten die Weibchen signifikant die markierten Pflanzen. Die Differenzierung von markierten und unmarkierten Pflanzen kann dabei nur aufgrund der olfaktorischen Signale erfolgt sein, da die jeweils zur Wahl stehenden Pflanzen weder in der Höhe, noch im Verzweigungsgrad, noch in der Anzahl der Blütenknospen unterschiedlich waren. Die Wahl der Weibchen für eine Wirtspflanze hing somit von der Wahl der Männchen für ein Territorium ab. Dieses Ergebnis ist besonders für die Evolution bedeutsam, denn die Männchen wählen dadurch die Wirtspflanze für den Nachwuchs ihres Vorgängers aus. Interessanterweise bevorzugten die Männchen ebenfalls Pflanzen, die von Artgenossen markiert worden sind.
- An der Ovipositorspitze besitzen die Weibchen von *U. cardui* ein rezeptives Feld mit mehreren, morphologisch unterschiedlichen Rezeptoren. Hauptsächlich scheinen sie sowohl mechanorezeptive, sowie chemorezeptive Funktionen zu haben. Nach ähnlichen Studien in anderen Insektenarten ist es auch denkbar, dass die Rezeptoren in der Lage sind den Wassergehalt des Gewebes zu bestimmen. Die Weibchen sind in der Lage, mit Hilfe des rezeptiven Feldes die innere Struktur der Seitenknospe zu analysieren.
- Es konnte nachgewiesen werden, dass der Durchmesser des Wachstumspunktes der jeweiligen Seitenknospe einen signifikanten Einfluss auf die Wahl des

Eiablageortes der Weibchen hatte. Seitenknospen mit einem Durchmesser des Wachstumspunktes von über 0.62mm haben eine höhere Wahrscheinlichkeit, dass sie für die Eiablage ausgewählt werden. Die Gelegegröße wurde von den Weibchen dem Durchmesser des Wachstumspunktes angepasst. Dies deutet darauf hin, dass die Weibchen in der Lage sind, die Qualität der betreffenden Seitenknospe, die sich auf die Überlebenswahrscheinlichkeit der Larven auswirkt, abzuschätzen.

Diese Ergebnisse wurden in einem allgemeinen Modell der „foraging-strategy“ von *U. cardui,* als ein Beispiel für die Wirtspflanzenwahl eines spezialisierten herbivoren Insektes, zusammen gefasst.