Mosquitoes as a Part of Wetland Biodiversity

BY

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Abstract
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Wetlands contain both aquatic and terrestrial environments which generates high biodiversity. However, they are commonly associated with mosquitoes (Diptera: Culicidae), and mosquitoes are usually regarded as negative by humans because they can cause nuisance and transmit diseases. This thesis aimed to clarify the association between mosquitoes and wetlands and to achieve a more balanced view of biodiversity in wetlands by including mosquito diversity.

Studies on adult mosquito diversity and assemblages were performed in 18 wetlands spread over Sweden. The Swedish mosquito species were organized in ten functional groups based on four life-history characteristics. This classification was used as an additional diversity measurement and as a tool for presentation of mosquito data.

Mosquito diversity showed several of the well-established diversity patterns such as a latitudinal gradient, a species-area relationship and a distribution-abundance relationship. In a landscape perspective, diversity of both mosquitoes and dytiscids (Coleoptera: Dytiscidae) were positively influenced by a high proportion of permanent water and a high amount of open areas, indicating co-varying diversity patterns.

Mosquito assemblages in the Nedre Dalälven region were mainly structured by the extent of flooded areas and wetland type (wet meadow, swamp and bog). In addition to the influence of the proportion of temporary wetlands at a local scale, the proportion of forest gained importance at larger spatial scales and in relation to dispersal distances of species. In southern Sweden, mosquito faunas differed between natural and constructed wetlands, partly reflecting differences in wetland size. In an experiment, different responses of two co-occurring mosquito species to rapid larval habitat desiccation indicate that weather conditions after a flood could influence mosquito assemblages.

The conclusions of this thesis provide suggestions on how to construct and position wetlands for increased insect diversity, and indicate that low abundance of major nuisance species might be crucial for acceptance of wetlands near human settlements.

Keywords: diversity patterns, species assemblages, functional groups, constructed wetlands, dytiscids

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"Jag letar efter formeln som gör vardagen till helg
en solskensblick som håller sikten klar.
En jägare som jagar myggor fäller ingen älg
men en och annan tråkig kommentar."

Claes Pihl 2003, "Räta linjens ekvation"

List of Papers

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

I   Schäfer M & Lundström JO (2001). Comparison of mosquito (Diptera: Culicidae) fauna characteristics of forested wetlands in Sweden. Annals of the Entomological Society of America 94, 576-582.

II   Schäfer ML, Lundström JO & Petersson E. Variation of mosquito (Diptera: Culicidae) assemblages in relation to wetland type and water regime in Central Swedish wetlands. Submitted manuscript.

III   Schäfer ML, Lundkvist E, Landin J, Persson TZ & Lundström JO. Influence of landscape variables at different spatial scales on mosquito (Diptera: Culicidae) and dytiscid (Coleoptera: Dytiscidae) faunas in Swedish wetlands. Submitted manuscript.

IV   Schäfer ML, Lundström JO, Pfeffer M, Lundkvist E & Landin J (2004). Biological diversity versus risk for mosquito nuisance and disease transmission in constructed wetlands in southern Sweden. Medical and Veterinary Entomology 18, 256-267.

V   Schäfer ML & Lundström JO. Different responses of two flood-water mosquito species *Aedes vexans* and *Ochlerotatus sticticus* (Diptera: Culicidae) to larval habitat drying. Manuscript.

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Cover painting by Jan O. Lundström.

Contents

Introduction

Biodiversity

The term "biodiversity" is usually used as a synonym for "variety of life" and is widely applied not only in scientific context but also in media and political discussions (Gaston 1996). Biodiversity ranges from the level of genes over species to ecosystems. The variety of life forms has long been a source of amazement and scientific curiosity (Tilman 2000), but the question of how many species there are will probably never be answered. Recent estimates of the total number of species on earth (considering only eukaryotic organisms) vary between 5-15 million (May 2000). However, calculations show that species currently disappear at rates of at least several hundred times the rate expected on the basis of geological records (Dirzo and Raven 2003). The predominant cause of extinction is the loss of habitat as a result of human activities.

Most analyses of biodiversity (including those in this thesis) are performed at the species level (Dirzo and Raven 2003), and a number of patterns have been found. A well-established pattern is the increasing diversity of most organisms with decreasing latitude, resulting in maximum diversity at tropical latitudes (e.g. Gaston and Williams 1996). Another general accepted pattern is the species-area relationship, stating that the number of species will increase with area, based on the theory of island biogeography by MacArthur and Wilson (1967). Local diversity patterns are related to regional diversity by processes like source-sink population structures or metapopulation dynamics (Holt 1993). Numerous studies have addressed the relationships of species diversity with environmental variables, but generalizations from this work have been difficult (Gaston 1996). The importance of biodiversity for ecosystem processes has been the focus in studies on functional diversity, looking at the extent of functional differences among the species in a community (e.g. Collins and Benning 1996, Petchey and Gaston 2002).

Does biodiversity matter? This question needs to be addressed in order to motivate people to care and take action. There have been suggestions to put a price on the value of species and ecosystem services since this would give ecologists stronger arguments in discussions with policy makers (Kunin and

Lawton 1996). In an attempt to do so, Constanza et al. (1997) estimated the economic value of ecosystem services globally to be an average of 33 trillion US Dollars per year. Services provided by ecosystems include climate regulation, nutrient cycling, water supply, food production, pollination and recreation.

Wetlands

Wetlands are important ecosystems providing services like waste treatment, water supply, disturbance regulation, and recreation. Continuing the idea of setting a value to ecosystem services, the world's wetlands provide services worth 4.9 trillion US Dollars per year (Constanza et al. 1997).

Productivity of wetlands is high compared to other ecosystems, and they also provide habitat for a wide range of species (Mitsch et al. 1994, Keddy 2000). Wetlands contain features of both terrestrial and aquatic environments, occurring along a soil moisture gradient from water to dry habitats (Sharitz and Batzer 1999). Thus, wetland organisms have to cope with varying conditions of either wet or dry habitat. Wetland plants need to tolerate hypoxic soil conditions caused by flooding, which is achieved by the presence of lacunae (aerenchyma) or by modification of metabolic pathways (Keddy 2000). In contrast, wetland animals, in particular invertebrates, have developed strategies to tolerate desiccation, often by drought-resistant eggs (e.g. various crustaceans and dipterans) or by burying themselves in the mud (e.g. some beetles). Many wetland animals have the advantage of being mobile and can thus avoid unfavourable conditions by dispersal and recolonization (e.g. Batzer and Wissinger 1996, Wissinger 1999).

A serious problem when comparing wetland studies is the lack of a generally accepted definition of a wetland and a wetland classification. Keddy (2000) points out that that there are at least two kinds of wetland definitions for different purposes, the scientific and the legal one. He defines a wetland as an "ecosystem that arises when inundation by water produces soils dominated by anaerobic processes and forces the biota, particularly rooted plants, to exhibit adaptations to tolerate flooding". Also, the terminology for describing wetlands varies both among human societies and among their scientific communities (Keddy 2000). Wetlands comprise a variety of habitat types, like river deltas and inundation areas, marshes, peatlands, and swamps (Mitsch et al. 1994). Even though global classification systems exist, like the system of the "Convention on Wetlands of International Importance, especially as Waterfowl Habitat" (usually referred to as the Ramsar Convention) (Scott and Jones 1995), their scientific application is somewhat limited. In this thesis, I used the more practical approach suggested by Keddy (2000), consisting of six basic wetland types. These are swamp, marsh, bog, fen, wet meadow and shallow water (see also Materials and Methods).

Even though wetlands cover an area of approximately 7-8 million square kilometres worldwide, they are a threatened landscape (Mitsch et al. 1994). In industrialized countries, it has been a long tradition to drain wetlands to increase areas for agriculture and forestry, and to regulate water-flow in streams and rivers to minimize flooding and to produce power. Historically, draining of wetlands was also conducted to reduce control malaria and other mosquito-borne diseases (Willott 2004). All these human activities have strongly reduced the number of wetlands and the total wetland area. In the eighties, finally the importance of wetland ecosystems became more widely acknowledged, resulting in a worldwide trend of restoring and constructing wetlands (Mitsch et al. 1994, Perry and Vanderklein 1996).

Wetlands in Sweden

About 30% of the land surface in Sweden has been covered by various types of wetlands (Sjöberg and Ericson 1997). Drainage activities in the 19th and 20th century have reduced this area to approximately three fourths of it. Wetland reduction has been more substantial in the southern and central part of the country than in the less populated northern part. In southern Sweden, up to 90% of former wetland areas has disappeared (Svensson and Glimskär 1993). In total, about 3 million ha of various wetland types (wet meadows, bogs, swamps, small waters) have been converted (Leonardsson 1994). About 9.3 million hectares of wetland area remain, but they consist mainly of bogs and swamps located in the boreal part that has been less intensively utilized (Sjöberg and Ericson 1997). In addition to drainage activities, wetlands are threatened by water regulation of large rivers. About 70% of the rivers in Sweden are regulated for power production (Ministerrådet and Naturvårdsverket 2003).

In recent years, drainage activities have been reduced and are nowadays legally forbidden in about 40% of Sweden's area, mainly in the southern part (Ministerrådet and Naturvårdsverket 2003). Legal protection of wetlands has also increased. Many wetlands are protected as Nature Reserve and National Park, most of which are also included in the European network Natura 2000 (Naturvårdsverket 1997). In addition, wetlands have been restored and constructed, in particular for nutrient retention or as habitat for water fowl (Svensson and Glimskär 1993). During the last years, approximately 3300 ha of new wetlands were constructed in Sweden (information from www.naturvårdsverket.se).

Mosquitoes

Among the most obvious inhabitants of wetlands are mosquitoes, the family Culicidae in the order Diptera, with about 3200 species worldwide. Mosquitoes are found throughout the world except the Antarctic (Lehane 1991). The literature on mosquitoes is extensive and the following general description of mosquito ecology is based on a number of references (Mohrig 1969, Gutsevich et al. 1974, Tempelis 1975, Wood et al. 1979, Lehane 1991, Kettle 1995, Schaffner et al. 2001, Becker et al. 2003).

Mosquito species can lay their eggs on the water surface (e.g. *Culex* or *Anopheles* species) or on moist soil that is subsequently flooded (e.g. *Aedes* or *Ochlerotatus* species). The larvae are truly aquatic and take oxygen from the water surface, except the larvae of the genera *Coquillettidia* and *Mansonia* that get their oxygen supply from aquatic plants like reed or cattail. These larvae attach themselves to the plant tissue and live submerged. Mosquito larvae feed mainly on bacteria, algae, protozoa and detritus. However, larvae of the genus *Toxorhynchites* are predacious and feed on other insects. The mosquito pupa is also aquatic and, in contrast to pupae of many other insects, rather mobile. The adults finally leave the aquatic habitat and occupy the terrestrial environment. Mating occurs shortly after adult emergence. In most mosquito species, females need a blood meal to complete development of the eggs, but in some species (e.g. in the genus *Toxorhynchites*) females produce eggs without blood intake. Preferred blood meal hosts differ among species. Most mosquito species take blood primarily from mammals (including humans) or birds, but some bite reptiles, amphibians, or even fish. The need for a blood meal is accompanied by an elaborate host-seeking behaviour as well as dispersal. As an energy source for flight, both female and male mosquitoes are dependent on plant nectar.

Mosquitoes have become famous due to the annoyance they can cause as well as their potential to transmit diseases. Mosquitoes are the vectors of a variety of hazardous diseases, including malaria, yellow fever, and dengue fever (Kettle 1995). Their role in human history is reflected in a book by Spielman and D'Antonio (2001) with the title "Mosquito. The story of man's deadliest foe", and in the preface it reads:

> "No animal on earth has touched so directly and profoundly the lives of so many human beings. For all of history and all over the globe she has been a nuisance, a pain, and an angel of death. Mosquitoes have felled great leaders, decimated armies, and decided the fates of nations."

Returning to the association of mosquitoes and wetlands, this is truly a controversial relationship, summarized in the words by Mitsch (1994) that one of the original causes of the incompatibility of human cultures and wetlands in many parts of the world is the mosquito. With this background it is not

surprising that most studies on wetlands and mosquitoes deal with measurements to reduce the number of mosquitoes (e.g. Batzer and Resh 1992, Tennessen 1993, de Szalay et al. 1995, Walton and Workman 1998, Walton et al. 1998).

However, when biodiversity is studied in wetlands, mosquitoes are rarely a target group. Such studies focus more on "nice" animals like birds, amphibians, dragonflies and diving beetles (Chovanec 1994, Chovanec and Raab 1997, Worrall et al. 1997, Melvin and Webb 1998, Lundkvist et al. 2001). In this thesis, the unusual connection of mosquitoes, wetlands and diversity was considered. Diving beetles were however included in one of the studies to compare diversity patterns of mosquitoes and diving beetles.

Mosquitoes in Sweden

The list of Swedish mosquitoes includes 47 species, covering the six genera *Anopheles* (6 species)*, Culex* (3 species)*, Culiseta* (7 species)*, Coquillettidia* (1 species)*, Aedes* (4 species) and *Ochlerotatus* (26 species) (from Schaffner et al. 2001)*. It should be noted that the genus *Ochlerotatus* used to be included as a subgenus in the genus *Aedes* but was lifted to genus level in 2000 (Reinert 2000). A first monograph on Scandinavian mosquitoes was provided by Natvig (1948). The geographic distribution of mosquito species in Sweden has been summarized by Dahl (1974, 1977). Also, information on life-history and ecological requirements is available for many Swedish mosquito species (see below) which provided a profound background for the studies in this thesis.

In the eighties, mosquitoes received increased attention due to their role in transmission of the Sindbis virus. This virus causes Ockelbo disease in humans, with symptoms of arthralgia, rash and fever. Many studies were performed to gather information on mosquito feeding and activity patterns, and to identify mosquito vectors (Niklasson et al. 1984, Jaenson and Niklasson 1986, Jaenson et al. 1986, Jaenson 1988, Francy et al. 1989, Lundström et al. 1990, Lundström et al. 1990, Turell et al. 1990). *Culex torrentium* was identified as the main enzootic vector of Sindbis virus among birds, and *Aedes cinereus* was recognized as the main link vector for transmission of Sindbis virus from viremic birds to humans. Mosquitoes are also suspected to play a role in transmission of the bacteria *Francisella tularensis* causing Tularaemia in humans (Mörner 1992, Eliasson et al. 2002).

Sweden has a reputation for the fabulous mosquito annoyance encountered during the summer, especially in northern localities. Returning to the connection of mosquitoes and wetlands, and considering the fragile status of wetlands, it seems important to clarify this association. The studies in this thesis therefore aimed to evaluate mosquito diversity and assemblages in relation to selected environmental variables, and thereby achieve a better

understanding of the mosquito-wetland association. The intention was a more balanced view of biodiversity in wetlands by including organisms that may be considered negative or harmful to humans. Addressing this aspect of wetlands instead of neglecting it could reduce the risk for a negative backlash in the positive trend of protecting, restoring and constructing wetlands.

Materials & Methods

Study areas

Study areas were spread over Sweden, ranging from Abisko in the north to Egeside in the south (Figure 1). Altogether, 18 wetlands were included. They differ from each other in many aspects, and the main characteristics are summarized in Table 1. Wetland type is given according to Keddy (2000), with the following six types:

- swamp: dominated by trees rooted in hydric soil, but not in peat
- marsh: dominated by herbaceous plants rooted in hydric soils but not in peat
- bog: dominated by *Sphagnum* moss, sedges, Ericaceous shrubs or evergreen trees rooted in deep peat
- fen: dominated by sedges and grasses rooted in shallow peat, often with considerable water movement through the peat
- wet meadow: dominated by herbaceous plants rooted in occasionally flooded soils
- shallow water: dominated by truly aquatic plants growing in and covered by at least 25 cm of water

A natural wetland is often dominated by one wetland type and includes patches of other wetland types. I classified 14 out of my 18 study areas by one main wetland type while the remaining four were characterized by two main wetland types. The 13 natural wetlands included mainly swamp (5), wet meadow (2), fen (1), bog (2), swamp and bog (2), and swamp and wet meadow (1). The five constructed wetlands were classified as swamp (1), marsh (2), shallow water (1) and marsh and wet meadow (1). These five wetlands were constructed for different purposes including habitat for water fowl, nutrient retention, storm water retention and water power.

The main vegetation types in the wetlands are given according to Påhlsson (1998). In this classification of Nordic vegetation, seven major vegetation groups are presented: alpine, forest, mire, sea shore, open cultivated, freshwater, and terrain-and substrata dependent vegetation. These main groups are then further divided into more specific vegetation types.

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Table 1. The main characteristics of the 18 study areas in Sweden

region	study area	origin	main wetland type	main vegetation type	paper
Northern Sweden	1) Abisko	natural	swamp, bog	mountain birch forest of dwarf shrub-grass type	I
	2) Allavaara	natural	swamp, bog	mountain birch forest of low herb type	I
	3) Bergsåker	natural	swamp	alder forest of wet herb type	I
Nedre Dalälven	4) Sälja	natural	wet meadow	tall sedge-herb variant	II, III
	5) Hadeholm	natural	wet meadow	tall sedge-herb variant	II, III
	6) Valmbäcken	natural	swamp	alder forest of wet herb type	II
	7) Fågle	natural	swamp	alder forest of wet herb type	II, III
	8) Karinmossen	natural	bog	pine of dwarf shrub type, hare's tail cotton grass-Sphagnum type	II, III
	9) Tavelmuren	natural	bog	pine of dwarf shrub type, hare's tail cotton grass-Sphagnum type	II, III
Linköping	10) Stavsätter-old	natural	swamp	mixed forest of wet herb type	III, IV
	11) Stavsätter-new	constructed	shallow water	common club-rush type, tufted hair-grass meadow type	III, IV
Halmstad	12) Stjärnarp-old	constructed	swamp	mixed forest of wet herb type	III, IV
	13) Stjärnarp-new	constructed	marsh, wet meadow	bulrush type, tufted hair-grass meadow type	III, IV
	14) Vallås	constructed	marsh	bulrush type	IV
Hässleholm	15) Gullarparsjön	natural	fen	purple moor grass meadow type	IV
	16) Nöbbelöv	natural	swamp	alder forest of wet herb type	IV
	17) Magle	constructed	marsh	bulrush type	IV
Kristianstad	18) Egeside	natural	swamp, wet meadow	mixed forest of wet herb type	I, IV

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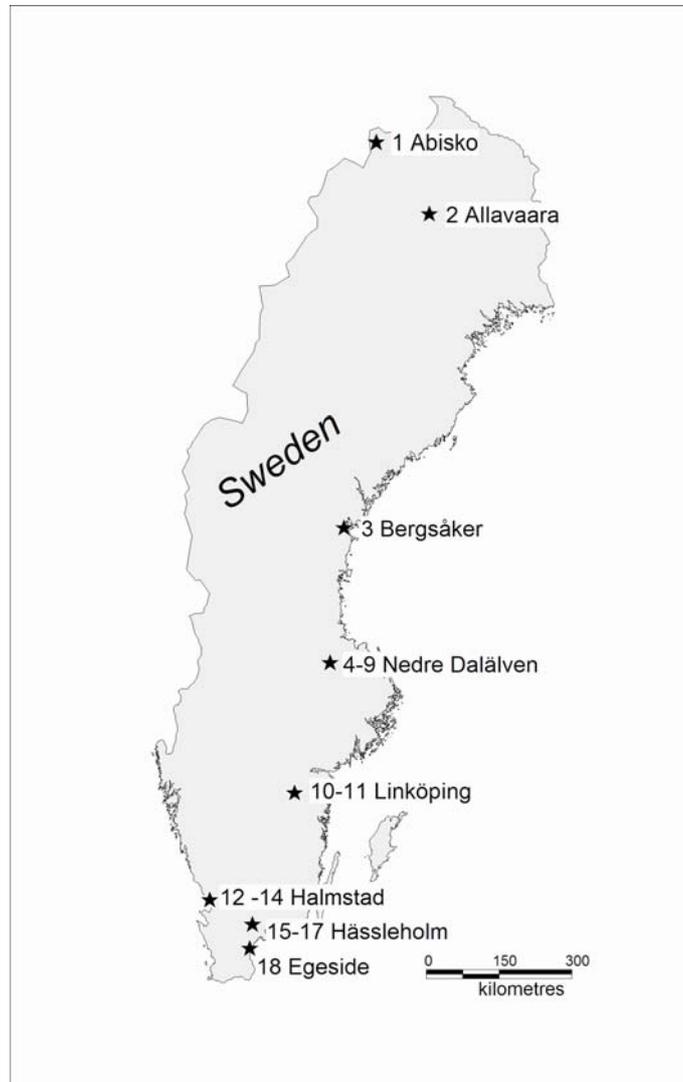
Figure 1.   Geographical location of the 18 study areas in Sweden.

Sweden has mainly a temperate climate with subarctic conditions in the very northern part. Most of the country is covered by snow during the winter months which results in snow melt ponds and pronounced spring floods around rivers and lakes in springtime (April to June, depending on latitude). Occasionally, heavy rainfall at other seasons can increase the water level in wetlands, especially in wetlands located in the inundation areas of large rivers.

Additional geographic information

The position of trap sites was measured using a differential Global Position-ing System (DGPS). Occasionally, extent of temporarily flooded areas was measured as well. All geographical information was handled in the software MapInfo Professional 7.0. (MapInfo Corporation 1985-2002), using vector-ized maps based on a scale of 1:50,000 (Geografiska Sverigedata, Lant-mäteriet, Gävle, Sweden).

In paper II, temporal variations of flooded wetland areas in the Nedre Dalälven region were calculated using a digital terrain model (DTM). The elevation data for the DTM originated from laserscanning of the Nedre Dalälven region by airplane in May 2003 (Fotonor AS, Sandvika, Norway and BlomInfo AB, Stockholm, Sweden). Data was handled in the software Vertical Mapper 3.0 (MapInfo Corporation 2003) and MapInfo Professional 7.0 (MapInfo Corporation 1985-2002).

In paper III, the influence of landscape variables on mosquitoes and dytiscids was studied by drawing nested circles around the combined trap sites of each study area, with a radius of 100 m, 500 m, 1000 m, 2000 m and 3000 m. Within each ring (0-100 m, 100-500 m etc.), the area covered by permanent water bodies, temporary wetlands, forest and open land was measured in hectares. This geographic information was summarized in an index of water permanence and an index of shading. The water permanence index was calculated as the area covered by permanent water bodies divided by the sum of permanent water body area and temporary wetland area. The shading index was calculated by dividing the area covered by forest with the sum of area covered by forest and area covered by open land. The design was nested and the indices were summed up with increasing distance.

Collection methods

Mosquitoes

All field investigations focused on adult female mosquitoes, mainly because they are responsible for colonization and nuisance problems. Larvae were not included in the sampling schedule for several practical reasons. Sampling of adults can be more standardized than for larval stages (Service 1993, Renshaw et al. 1995), and identification of adult females is more reliable than identification of larvae in many cases. In addition, small larval stages are not identifiable at all.

In all collections, I used Centers for Disease Control (CDC) miniature light traps, with carbon dioxide in the form of dry ice as attractant (Fig. 2). Even though all kind of trap collections are biased, this method samples a large variety of mosquito species (Service 1993). The traps were placed in trees approximately 1.5 m above ground. They were activated early in the

Figure 2. CDC miniature light trap with dry ice as an attractant (in the paper bag behind the trap). In the net some captured mosquitoes can be seen. This trap is positioned in Österfärnebo, Central Sweden. Photo by JO Lundström.

evening for 12–14 hours duration until the next morning. Collected mosquitoes were anaesthetized with carbon dioxide, dispensed into plastic ampoules and immediately killed by freezing on dry ice. They were stored on dry ice and at -70°C until identification.

During the process of identification mosquitoes were kept cold (approximately 0-4°C) on a chill table. Mosquitoes were identified to species with keys by Mohrig (1969), Gutsevich et al. (1974), and Wood et al. (1979), while nomenclature followed Reinert (2000). All identified mosquitoes were or will be processed for virus isolation following the procedure by Francy et al. (1989) looking for cytopathogenic effects in cell cultures. Results from virus isolation are only included in the comparison of mosquito faunas from natural and constructed wetlands (paper IV).

The sampling effort for mosquitoes in the different study areas is summarized in Table 2. In each month, sampling was conducted on three consecutive nights except for the six study areas in the Nedre Dalälven region. There, sampling was reduced to two consecutive nights per month due to very high numbers of mosquitoes.

Table 2. Summary of the sampling effort for mosquitoes in 18 study areas in Sweden

study area	year of sampling	month	no. of traps	total no. trap nights	paper
1)Abisko	1996, 1997	July, August	6	36	I
2)Allavaara	1991	June, July	3	27	I
3)Bergsåker[*]	1985	June-August	6	36	I
4)Sälja	2000,2001,2002	May-September	3	84	II, III
5)Hadeholm	2000,2001,2002	May-September	3	84	II, III
6)Valmbäcken	2000,2001	May-September	3	66	II
7)Fågle	2000,2001,2002	May-September	3	84	II, III
8)Karinmossen	2000,2001,2002	May-September	3	84	II, III
9)Tavelmuren	2000,2001,2002	May-September	3	84	II, III
10)Stavsätter-old	1999	June-September	3	36	III, IV
11)Stavsätter-new	1999	June-September	3	36	III, IV
12)Stjärnarp-old	1999	June-September	4	48	III, IV
13)Stjärnarp-new	1999	June-September	2	24	III, IV
14)Vallås	1999	June-September	3	36	IV
15)Gullarparsjön	1999	June-September	3	36	IV
16)Nöbbelöv	1999	June-September	3	36	IV
17)Magle	1999	June-September	3	36	IV
18)Egeside	1998	June-August	3	27	I, IV

* data based on the study by Francy et al (1989).

Diving beetles

In one study (paper III), adult diving beetles (Coleoptera: Dytiscidae) were sampled in addition to mosquitoes. The family Dytiscidae is represented in Sweden by 149 species in 27 genera (Nilsson and Holmen 1995). All adults are aquatic, but may leave the water for migration or for overwintering on land. Many diving beetles are good fliers, but some species lack flight ability due to reduction or absence of wings or wing muscles (Jackson 1956). Diving beetles are often among the first large invertebrate predators that arrive in newly-formed wetlands (Layton and Voshell 1991). Many diving beetles are reported to feed on mosquito larvae (Service 1973, Onyeka 1983, Nilsson and Söderström 1988, Nilsson and Svensson 1995). Their importance as a natural control on mosquito larvae has been studied (Lundkvist et al. 2003) but the results are inconclusive and more studies are needed. Both mosquitoes and diving beetles utilize the aquatic and terrestrial environment of wetlands, they occur in many types of water bodies and are early colonizers of new wetlands. I compared diversity patterns of these two insect families in a study on the effect of landscape variables.

Collections of diving beetles were conducted using activity traps. They consist of a 1.5 l plastic jar, equipped with a funnel (100 mm at widest point, 23 mm at narrowest point) in the bottom and a net lid (0.5 mm mesh size) on

Table 3. Summary of the sampling effort for diving beetles in nine wetlands in Central and Southern Sweden

study area	year of sampling	month of sampling	no. of traps	total no. of trap days	paper
4)Sälja	2002	May-August,	3	54	III
5)Hadeholm	2002	May-August	3	96	III
7)Fågle	2002	May-August	3	28	III
8)Karinmosse	2002	May-August	3	80	III
9)Tavelmuren	2002	May-August	3	82	III
10)Stavsätter-old	1996, 1997	April, June, July	3	180	III
11)Stavsätter-new	1997	April, June, August	5	145	III
12)Stjärnarp-old	1989,1999	May, July	30	120	III
13)Stjärnarp-new	1989,1999	May, July	30	120	III

the opposite side to allow water exchange (Lundkvist et al. 2001). These traps are considered efficient for collecting diving beetles of different sizes (Hilsenhoff and Tracy 1985, Hilsenhoff 1991). Traps were placed horizontally on the bottom in shallow water. In permanent water bodies, trap sites were located near the shoreline, whereas traps in temporary water bodies were restricted to sites with sufficient water depth. Adult beetles were sorted out in the field, preserved in 80% ethanol, and later identified to species in the laboratory. Information and identification keys for Scandinavian diving beetles are provided by Nilsson and Holmen (1995).

Diving beetles were collected in nine study areas and the sampling schedule is summarized in Table 3.

Data analysis

The available information on life-history of most Swedish mosquito species was used for a classification of species into functional groups. The objectives of the classification were to provide a measurement of diversity in addition to species richness, and to have a tool for mosquito data presentation to non-specialists. The classification was first developed based on six life-history characteristics, including oxygen source for larvae, oviposition sites, overwintering life stages, preferred blood meal hosts, preferred larval habitat and number of generations per year. This resulted in 14 functional groups (paper I). Since oxygen source for larvae provided only additional information for existing groups and only inconsistent information was available for preferred larval habitat, these two characteristics were excluded in a later version (paper IV). This resulted in the ten refined functional groups that are presented in Figure 3.

oviposition sites   overwintering stage   preferred blood meal host   no. of generations   species   group no.

			univoltine	*Cq. richiardii*	1a
	larvae	mammals			
			multivoltine	*An claviger*	1b
				An. maculipennis s.l.	1c
				Cs. annulata	
		mammals	multivoltine	*Cx. pipiens molestus*	
water				*Cs. alaskaensis**	
				Cs. bergrothi*	
	females			*Cs. subochrea**	
		birds	multivoltine	*Cx. pipiens pipiens*	1d
				Cx. torrentium	
		amphibians	multivoltine	*Cx. territans*	1e

				Oc. annulipes	2a
				Oc. cantans	
				Oc. cataphylla	
				Oc. communis	
				Oc. cyprius	
				Oc. diantaeus	
				Oc. excrucians	
				Oc. flavescens	
			univoltine	*Oc. hexodontus*	
				Oc. impiger	
				Oc. intrudens	
				Oc. leucomelas	
				Oc. nigripes	
	eggs	mammals		*Oc. pionips*	
				Oc. pullatus	
				Oc. punctor **	
				Oc. riparius	
				Ae. cinereus	2b
				Ae. rossicus	
				Ae. vexans	
land			multivoltine	*Oc. caspius*	
				Oc. detritus	
				Oc. dorsalis	
				Oc. sticticus	
	eggs (larvae)	mammals	multivoltine	*Oc. geniculatus*	2c
				An. plumbeus	
		mammals	univoltine	*Oc. rusticus*	2d
	larvae (eggs)			*Cs. fumipennis*	2e
		birds	univoltine	*Cs. morsitans*	
				Cs. ochroptera**	

Figure 3. The mosquito species of Sweden organized into ten functional groups based on four biological characteristics. *maybe univoltine in the north ** two generations have been observed. *Ae.=Aedes, An.=Anopheles, Cq.=Coquillettidia, Cs.=Culiseta, Cx.=Culex, Oc.=Ochlerotatus*

Mosquito species are first sorted into two groups, depending on if eggs are laid on water (group 1) or on land (group 2). Mosquitoes in group 1 inhabit all kinds of standing water bodies of relatively long duration, such as permanent ponds of varying sizes or water-filled tracks. In this group two species with overwintering larvae can be found (groups 1a and b), while all other species overwinter as females. Groups 1a-c prefer mammals as blood meal hosts, while *Culex pipiens pipiens* and *Culex torrentium* in functional group 1d have birds as preferred blood meal hosts, and one species, *Culex territans* (group 1e) has amphibians as preferred blood meal hosts. Most species in group 1 can have more than one generation per year.

Mosquitoes of functional group 2 utilize water bodies of relatively short duration, such as snow-melt ponds or temporarily inundated wetlands. They lay their drought- and cold-resistant eggs on humid soil. The larvae hatch after subsequent flooding of the eggs. In functional group 2, most species overwinter as eggs, although some can also overwinter in the larval stage. Mammals are the preferred blood meal hosts for all species except for three ornithophilic *Culiseta* species in functional group 2e. Most species can be found in functional group 2a, the so-called snow melt mosquitoes that produce one generation per year during spring. Common species in group 2a include *Ochlerotatus cantans, Ochlerotatus communis, Ochlerotatus punctor* and *Ochlerotatus intrudens*. Functional group 2b, the so-called floodwater mosquitoes, can have more than one generation per year during spring and summer. Group 2b contains the major nuisance species due to their capacity to produce multiple generations that can result in very large numbers of individuals during the whole summer season. Especially *Aedes vexans* and *Ochlerotatus sticticus* have a reputation for their nuisance potential. The species in functional group 2c are specialized in having their larvae in tree holes.

For a few species, information on certain characteristics is scarce or there is more than one strategy. The species in group 2d and 2e can switch from overwintering in the larval stage to overwintering in the egg stage, in response to climatic conditions. In group 2e, *Culiseta ochroptera* has been reported to overwinter also as females (Gutsevich et al. 1974, Jaenson et al. 1984). Besides, some univoltine mosquitoes can sometimes have a small second generation after summer rains (Mohrig 1969, Gutsevich et al. 1974).

Some *Anopheles* and *Culex* species cannot be distinguished morphologically as females. *Anopheles maculipennis* sensu lato is a complex of four species in Sweden (Jaenson et al. 1986), but they all sort into the same functional group. *Culex pipiens/torrentium* is a complex as well, with *Cx. torrentium* and *Cx. pipiens pipiens* as bird-feeding species (group 1d), and *Cx. pipiens molestus* as an anthropogenous biotype (now usually refered to as *Cx. p. pipiens* biotype *molestus*) (group 1c). *Cx. pipiens* and *Cx. torrentium* cannot be reliably distinguished morphologically as adult females and larvae, whereas male hypopygia are different (Service 1968). *Cx. pipiens*

pipiens and *Cx. pipiens molestus* can only be separated by testing autogeny and stenogamy. In Sweden, there is only a single record of *Cx. pipiens molestus* (Natvig 1948), whereas *Cx. pipiens pipiens* and *Cx. torrentium* are reported regularly (Dahl 1977). Therefore, unspecified females of *Cx. pipiens/torrentium* were sorted in group 1d.

Mosquito sampling resulted in enormous numbers of individuals, and at times more than I had wished for. Identification of the whole catch was sometimes impossible, and in these cases extrapolation was used. The total number of individuals per trap and night was estimated by weighing, a sub-sample identified, and the proportion of each species extrapolated to the estimated total number.

Abundance was usually provided as the mean number of individuals per trap and night. Mosquito diversity was evaluated using a number of diversity indices in addition to species richness. In paper I, comparing mosquito faunas at a large geographical scale, I used the Shannon index, Simpson's index, and Q-statistics (for details see Magurran 1988, Krebs 1999). In paper III, alpha of the log-series and the reciprocal of Berger-Parker index are used, while alpha and Q-statistics were employed in paper IV. These indices show low sensitivity to sample size and good discriminant ability (Magurran 1988). In paper III, sample effort differed between the study areas and rarefaction was used to estimate the number of species for a standardized sample size. Diversity indices and rarefaction were computed in the software Ecological Methodology 5.1 (Krebs 1998) and Biodiv 5.1 (Baev and Penev 1995).

Ordination was used to evaluate the effect of environmental variables on species assemblages (ter Braak and Smilauer 2002). Either Canonical Correspondence Analysis or Redundancy Analysis were employed, depending on the species response curves (unimodal or linear). Mosquito species assemblages were compared using the Renkonen index (percentage of similarity) and the Bray-Curtis similarity coefficient for quantitative data and a subsequent cluster analysis.

Of course I am also aware that it is impossible to assess complete diversity of any group of organisms, and mosquitoes are no exception. Trap collections are biased and some species might be overrepresented while others might be underestimated or even missing. Nevertheless, since I applied the same sampling method in all areas, collected large numbers of individuals in most study areas, and spread the collections over the whole mosquito season, I believe that a representative fraction of the mosquito fauna has been assessed.

Survival strategies of mosquito larvae – an experiment

Mosquitoes as well as other insects using temporary ponds as larval habitats have to deal with the risk of desiccation of their larval habitat. Floodwater mosquitoes are extremely successful inhabitants of temporary wetlands and show several adaptations for a life in this unstable environment. I tested the hypothesis that floodwater mosquitoes would react to diminishing habitat by accelerating larval development time which would then result in smaller adults (paper V). Habitat drying also leads to increased larval densities in smaller water bodies, and I therefore included larval density as a factor in the experiment.

The experiment was set up as a two-way design with larval density and water level schedule as factors. Larval density included two levels, either one larva or 20 larvae. Water level schedule was represented by three levels, either constant, decreasing or decreasing followed by drying. This setup resulted in six treatments with 20 replicates each and a total of 1260 mosquito larvae. The mosquito larvae originated from two breeding sites close to the village of Österfärnebo in the Nedre Dalälven region, Central Sweden. They were sampled on 28 June, 2003, and larvae were not older than a couple of hours at the time of sampling. The experiment was started the same day.

The decreasing water level schedule was initiated on day four of the experiment, and on day six all water was removed in containers subject to drying. These containers were then regularly sprayed with water to keep some humidity in the soil. Surviving larvae were counted every second day from day 4 onwards. Occurrence of pupae as well as day of adult emergence was noted daily between day 9 and 14, and every second day afterwards. All adults were sexed and identified to species. Adult mosquito size was described by wing measurements (Renshaw et al. 1994). Response variables in the analysis were adult emergence day and wing length.

Results & Discussion

Altogether, 1,308,736 mosquitoes were sampled for this thesis. These collections included 35 of the 47 species reported from Sweden, and covered nine out of ten functional groups. The only group missing is functional group 1e, *Cx. territans*, a species with amphibians as preferred blood meal hosts. This species has nevertheless been collected in CDC traps in the Nedre Dalälven region (unpublished information), so absence of this species is not necessarily trap-related.

Patterns in mosquito diversity

A latitudinal gradient

The first analysis of mosquito diversity was looking at a gradient from northern to southern Sweden (paper I). Mosquito diversity, measured as species richness, number of functional groups and by three diversity indices, increased with decreasing latitude. A latitudinal diversity gradient is an established pattern for many organisms. In Northern Europe, such a pattern has been reported for terrestrial insects such as ants and saltatoria (bush-crickets, crickets and grasshoppers), as well as for insects with aquatic larvae such as dragonflies, stoneflies and aquatic beetles (Cushman et al. 1993, Väisänen and Heliövaara 1994, Heino 2002). Heino (2002) could also show a strong relationship between aquatic insect species richness and latitude with mean July temperature as an explanation for this pattern. Other supposed parameters producing latitudinal differences in species richness include differences in productivity or habitat heterogeneity (Rosenzweig 1995). Increasing habitat heterogeneity from northern to southern Sweden could be one explanation for the mosquito gradient, which was also reflected in the number of functional groups. Southern localities often provide more environmental variability with a larger variety of habitats, and they also had a higher number of functional groups. In addition, the biology of some species, e.g. overwintering in the larval stage, does not fit climatic conditions at northern localities.

In the analyses in paper I, only four wetlands are included. Looking at the summarized data from all study areas (Table 4), the general trend can still be seen, although with some exceptions.

Table 4. Number of mosquito species and functional groups and average number of individuals collected in the 18 study areas in Sweden. In study areas 4-9 where mosquitoes were sampled in more than one year, the range is given.

study area	no. species	no. functional groups	average no. individuals	paper
1)Abisko	10	2	415	I
2)Allavaara	12	2	352	I
3)Bergsåker[*]	16	6	435	I
4)Sälja	17-18	7	388-5709	II, III
5)Hadeholm	15-17	7	313-2281	II, III
6)Valmbäcken	16-18	7	4852-9257	II
7)Fågle	15-18	7	1170-4595	II, III
8)Karinmossen	15-17	7	481-2984	II, III
9)Tavelmuren	8-17	6-7	64-783	II, III
10)Stavsätter-old	15	7	44	III, IV
11)Stavsätter-new	11	7	5	III, IV
12)Stjärnarp-old	13	7	57	III, IV
13)Stjärnarp-new	12	7	9	III, IV
14)Vallås	15	7	61	IV
15)Gullarparsjön	17	8	201	IV
16)Nöbbelöv	16	7	203	IV
17)Magle	16	8	89	IV
18)Egeside	24	9	451	I, IV

* data based on the study by Francy et al (1989).

Forested wetlands in the Nedre Dalälven region (Valmbäcken, Fågle) are within the pattern. Further south, however, forested wetlands like Stavsätter-old and Nöbbelöv show lower species richness than expected for the latitude. Clearly, mosquito diversity does not depend solely on latitude. Looking at the most diverse southern wetland Egeside, this is a large wetland area with a complex environment providing a large variety of habitats, which is not the case at Nöbbelöv or Stavsätter-old.

Including previously published information on the geographical distribution of mosquito species in Scandinavia would add four species and one functional group (group 2b, *Ae. cinereus*) to our list for northernmost Sweden (Mehl et al. 1983, Andersson 1991). In an area near Bergsåker, Jaenson et al. (1986) sampled three additional species, including *Cx. territans* that feeds on amphibians. For southern Sweden, Dahl (1977) reported six more species which also included functional group 1e (*Cx. territans*), the only group missing from our collections in Egeside.

The species-area relationship

Another accepted pattern is the species-area relationship. Such a pattern was observed for nine wetlands in southern and south-eastern Sweden, including natural and constructed wetlands (Fig. 4). However, in this study, the num-

ber of species was also positively correlated with mosquito abundance which in turn was positively correlated with wetland size. For six wetlands in the Nedre Dalälven region, covering three wetland types, no species-area relationship was observed despite detailed data on flooded wetland area for four of the six wetlands (paper II). Lundkvist et al. (2001) did not find this pattern for diving beetles either. In contrast, March and Bass (1995) reported a positive species-area relationship for invertebrates in temporary pools. Bazzanti et al. (1996) studied invertebrates in an autumnal pond and found a positive relationship with temporal variations in pond area only for coleopterans and hemipterans.

It could be difficult to detect a species-area relationship for insects in wetlands because it can be difficult to define what wetland habitat is used by these specific insects, and then discriminate these wetland habitats sufficiently well for conducting area measurements. Working with mobile adult insects, this problem is even more obvious. In addition, habitat quality could be more important than size. According to Gaston and Blackburn (2000), one explanation for the species-area relationship could be an increase in the number of habitat types in parallel with area. If there is no increase in the number of habitat types with area, then no species-area relationship can be expected.
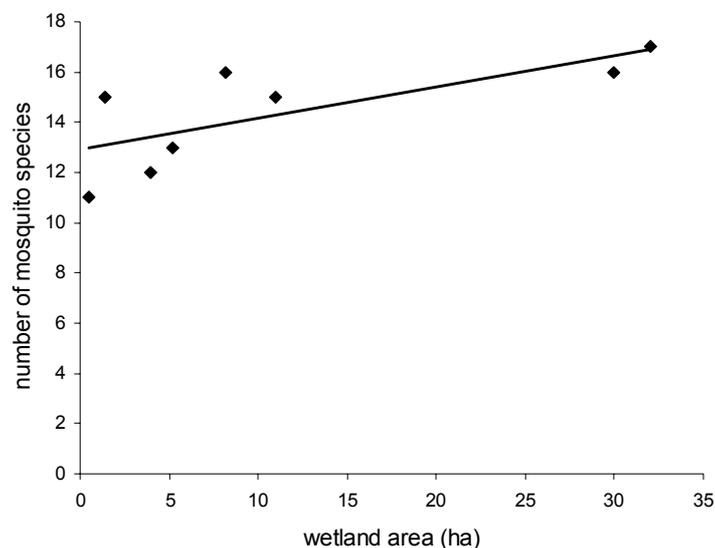
Figure 4. Positive relationship of mosquito species richness and wetland area based on data from eight wetlands in southern Sweden. The largest wetland from southern Sweden, Egeside Sjö (196 ha and 24 mosquito species), is not shown in this diagram.

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The distribution-abundance relationship

Beside the species-area relationship, the distribution-abundance relationship has received attention in ecological studies (Hanski and Gyllenberg 1997, Gaston et al. 2000). This relationship states that locally abundant species have a wider distribution range than rare species. In the study in the Nedre Dalälven region with six wetlands (paper II), mosquito species that were found in all six study areas were locally more abundant than species with a narrow distribution (Fig. 5). The same distribution pattern was found when looking at the three wetland types. Even though some rare species were found in all three wetland types, there was no abundant species recorded from only one wetland type. A positive distribution-abundance relationship has been observed in other studies on dipterans (Malmqvist et al. 1999, Hughes et al. 2000). The distribution-abundance relationship has been explained as a sampling artefact, but can also be due to metapopulation dynamics or ecological specialization (Hanski et al. 1993, Hanski and Gyllenberg 1997). According to the metapopulation dynamic model, locally common species become more widely distributed due to their low extinction rates and high colonization rates. Ecological specialization, based on Brown's niche breadth hypothesis, means that ecological generalists are both widely distributed and locally abundant while ecological specialists have a restricted distribution and low abundance.
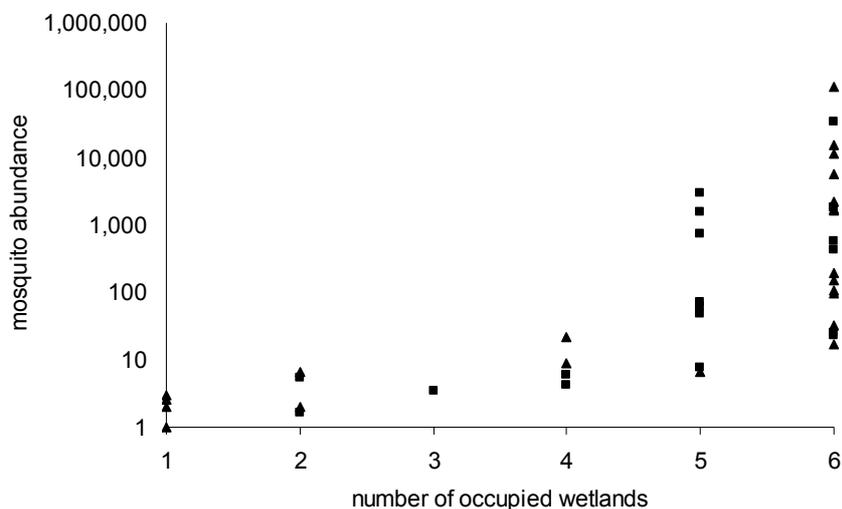
Figure 5. Positive distribution-abundance relationship for mosquito species collected in six wetlands in the Nedre Dalälven region in 2000 (triangles) and 2001 (squares).

Where is mosquito diversity high?

In addition of looking for general patterns, one can of course wonder if mosquito diversity is higher in wetlands with certain characteristics. Adult mosquito species richness did not differ significantly among three wetland types in the Nedre Dalälven region (paper II). Nevertheless, most mosquito species were found in the swamps, followed by the wet meadows, while the bogs had lowest species richness. Hughes et al. (2000) also found significantly higher dipteran species richness in aspen or meadow sites compared to conifer sites. Diversity indices for the mosquito data from the study areas in the Nedre Dalälven region showed highest diversity in the two wet meadows and in one of the bogs (paper III). However, all study areas in the Nedre Dalälven region were highly influenced by a single mosquito species, *Oc. sticticus*. The predominance of a single species results in high dominance and low diversity indices. Therefore, high diversity in these areas was mainly determined by low abundance of *Oc. sticticus.*

I also compared natural and constructed wetlands (paper IV). Species richness differed significantly among natural and constructed wetlands, but not diversity measured by Q-statistics and alpha of the log series. The number of mosquito species was higher in the natural than the constructed wetlands. In this study, I also found a positive species-area relationship. Therefore, this could be mainly a consequence of wetland size since most constructed wetlands are smaller than natural ones. Beaver et al. (1999) compared zooplankton and phytoplankton assemblages of constructed, impacted, non-impacted and temporary wetlands, but did neither find significant differences in species richness nor in diversity. Thus, constructed wetlands, despite their smaller size, can make important contributions to biodiversity, and in particular in a landscape perspective (Worrall et al. 1997, Semlitsch and Bodie 1998).

Highest number of species and functional groups of all study areas was found in the southernmost wetland Egeside Sjö (Table 4) and mosquito diversity measured by Q-statistics and alpha of the log series was also high in this area. Egeside Sjö is a large complex wetland with both forested and open parts. High environmental variability in combination with a mild climate is likely to be the cause for high mosquito diversity. A general positive association of insect diversity and habitat heterogeneity has been observed in a number of studies, mainly connected to variation in subhabitats and vegetation zones (see Wissinger 1999).

Co-varying diversity patterns of mosquitoes and diving beetles

In the study including both mosquitoes and diving beetles (paper III), I obtained the interesting result that diversity (measured as rarefaction of species richness for a standardized sample size and two diversity indices) of both mosquitoes and dytiscids was positively influenced by high water permanence and low forest shading (Fig 6). Mosquito diversity in this study was affected by high dominance of single species in temporary habitats. High dominance results in low diversity indices. Low diversity was thus associated with a high proportion of temporary wetlands (low permanence index), while high diversity was connected to high permanence. An increase in invertebrate diversity in wetlands with increasing pond duration has been observed in other studies (Higgins and Merritt 1999, Schneider 1999, Batzer et al. 2004). This could be explained by a permanence-predator gradient (Schneider and Frost 1996, Wellborn et al. 1996, Schneider 1999). In water bodies of short duration, only species with rapid growth and development and surviving hostile periods as desiccation-resistant eggs are found, and most predators are excluded. Increasing pond duration, however, allows colonization by predators and their influence on the invertebrate community structure increases. On the other hand, other studies found higher diversity in semi-permanent or seasonally flooded wetlands than in permanent water bodies and these results are explained by the "intermediate disturbance hypothesis" (Balla and Davis 1995, Evans et al. 1999, Whiles and Goldowitz 2001). In highly permanent habitats, top predators such as fish exclude other species while highly temporary habitats contain only rapid colonizers (Wissinger 1999, Whiles and Goldowitz 2001). Thus, diversity is highest in wetlands that are disturbed at intermediate frequencies (e.g. by occasional droughts). This hypothesis could hold for mosquito and dytiscid diversity as well, but was not tested in this thesis.

Similar responses of mosquito and dytiscid diversity could be an indication of co-varying diversity patterns among different organisms. Many studies have dealt with comparing diversity patterns of different organisms in order to find co-variation. It would make future biodiversity assessments for conservation issues easier if one group of organisms could be used as an indicator for diversity of more than this group. Some examples are reported. Kerr et al. (2000) found that lepidopterans could be used to predict richness of Hymenoptera in oak savannas in southern Ontario. Duelli and Obrist (1998) evaluated correlations of species numbers of higher taxonomic groups with total species numbers of arthropods and flowering plants. Their "top twenty" list of indicator groups favours Heteroptera, flowering plants, Symphyta and aculeate Hymenoptera as the best choice for biodiversity evaluation. For freshwater ponds, Briers and Biggs (2003) suggest Coe-

nagriidae (Odonata) and Limnephilidae (Trichoptera) as the best candidates for indicator taxa. For mosquitoes and dytiscids, more tests are needed to strengthen this first indication of co-varying diversity patterns.
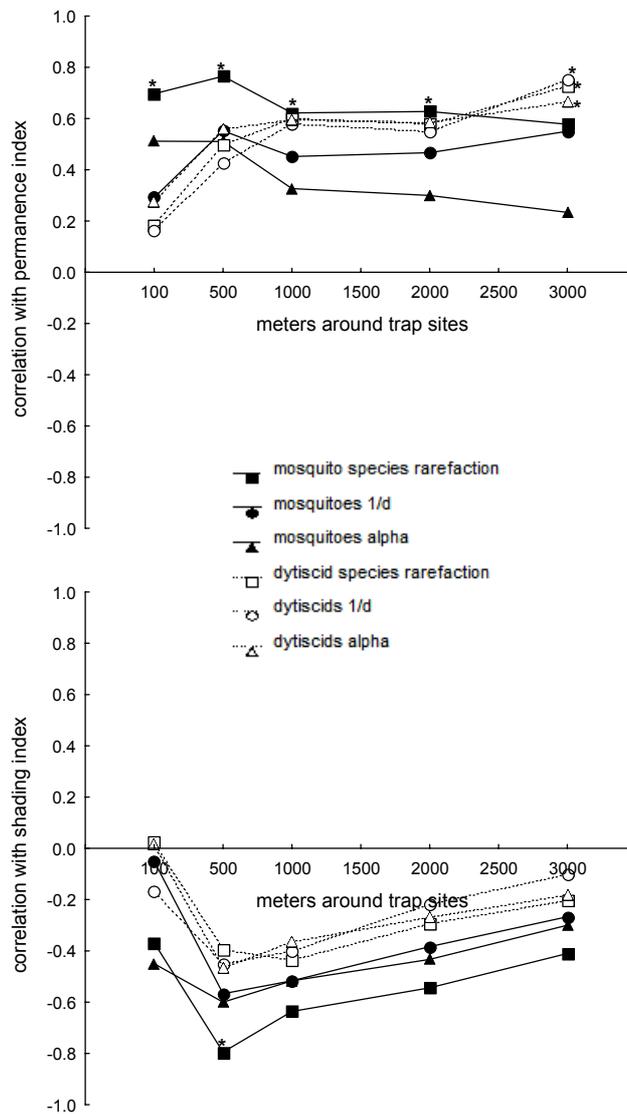
Figure 6. Spearman's rank correlation coefficient of mosquito and dytiscid diversity measured as species rarefaction, reciprocal of Berger-Parker index (1/d) and alpha of the log series with permanence indices (upper diagram) and shading indices (lower diagram) within five nested zones around trap sites in nine wetlands. Significant correlations ($p<0.05$) are marked with *.

Patterns in mosquito species assemblages

Assemblages of populations of different species living together in the same area result in communities. The communities have properties that are the sum of the properties of the individuals plus their interactions, and the interactions make the community more than just the sum of its parts (Begon et al. 1996). Diversity indices are one measure of community character, but can of course only be seen as abstractions of highly complex structures. Canonical ordination is widely used as a technique for relating the species composition of communities to their environment (ter Braak and Smilauer 2002). The result is an ordination diagram which displays how community composition varies with the environment. Thus, the output of the method depends largely on the input of appropriate environmental variables.

I employed ordination for mosquito species data in several studies. Environmental variables tested were a) wetland type, wetland size, extent of flooded area in the previous month, month of sampling and year of sampling for data from six wetlands in the Nedre Dalälven region (paper II), b) water permanence indices and forest shading indices within three spatial scales around trap sites for data from nine wetlands in southern and central Sweden (paper III), and c) origin of wetlands, wetland size and water permanence index for data from nine wetlands in southern Sweden (paper IV).

In all ordination diagrams, the mosquito species sorted according to functional groups (Figs. 7, 8 and 9). This indicates the ecological relevance of the functional group classification and strengthens this approach.

Month and year of sampling, extent of flooded area and wetland type

In the study in the Nedre Dalälven region, mosquito species assemblages were mainly influenced by month of sampling and year which together explained 65% of the total variation explained by all variables (Fig. 7). The seasonal variation of mosquito abundance is a rather well-documented pattern and can often be associated with weather and hydrological conditions (Jaenson et al. 1986, Margalit et al. 1987, Gleiser et al. 2002, Shaman et al. 2002, Zhong et al. 2003). In the Dalälven region, water regime of the River Dalälven is likely to be the main cause of variation in mosquito assemblages both during a season and between years. In 2000, high water level induced large flooded areas in both May and July, while in 2001 there was only one flood in May with a lower water level than in 2000. This was also reflected in the size measurements of flooded areas for wet meadows and swamps. The extent of flooded area in the previous month was an important variable in the ordination (excluding the two bogs) and together with month of sampling explained 81% of the total variance explained by all variables (Fig. 8). Hydroperiod is known to play an important role for invertebrate community
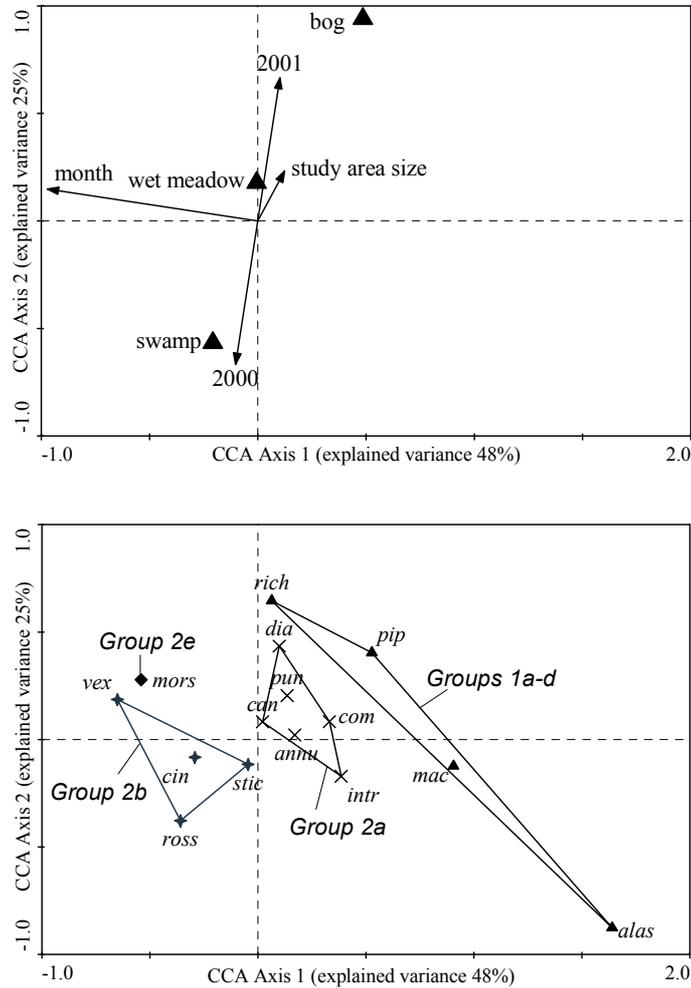
Figure 7. Mosquito species distribution in relation to environmental variables as determined by canonical correspondence analysis. The upper diagram shows the environmental variables. In the diagram below, the mosquito species distribution is shown, forming four clusters that correspond to functional groups. Data is based on mosquito collections from two years in six wetlands in the Nedre Dalälven region in Central Sweden. Species with less than 100 individuals in total are not shown in the diagram. Species abbreviations are explained in the appendix of paper II.

structures (e.g. Batzer and Wissinger 1996, Schneider 1999, Whiles and Goldowitz 2001). Mosquito assemblages are often particularly affected by large rivers with adjacent lowlands (Becker and Ludwig 1981, Vanhara 1991, Minar et al. 2001). Examples include the River Rhine in Germany, the

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River Morava in the Czech Republic and based on this thesis also the River Dalälven in Sweden.

Wetland type made up for most of the remaining variation of the adult mosquito assemblages while study area size did not add much to the model (Fig. 7). Habitat type seems to be biologically meaningful to many insect communities (Malmqvist et al. 1999, Hughes et al. 2000, Scott and Anderson 2002). Most community analysis for wetland organisms is based on aquatic invertebrates (e.g. Jeffries 1994, Bazzanti et al. 1996, Wellborn et al. 1996) but some use terrestrial adult insects. Garono and Kooser (1994) used ordination on data of adult trichoptera and also found an effect of wetland type. The same authors also tested if adult insect assemblages could be used to differentiate between wetlands and uplands (Garono and Kooser 2001). Ordination of terrestrial adult insect assemblages separated upland and wetland sites, and patterns could be related to vegetation structure. Schindler et al. (2003) could identify two adult dragonfly assemblages that were determined by water persistence and vegetation. In the Nedre Dalälven study, adult mosquito assemblages discriminated between three wetland types.

Mosquito assemblages in the Nedre Dalälven region were also affected by distance to other wetlands, since the dominating species *Oc. sticticus* is an excellent long-distance flyer that can be found at least 10 km away from its
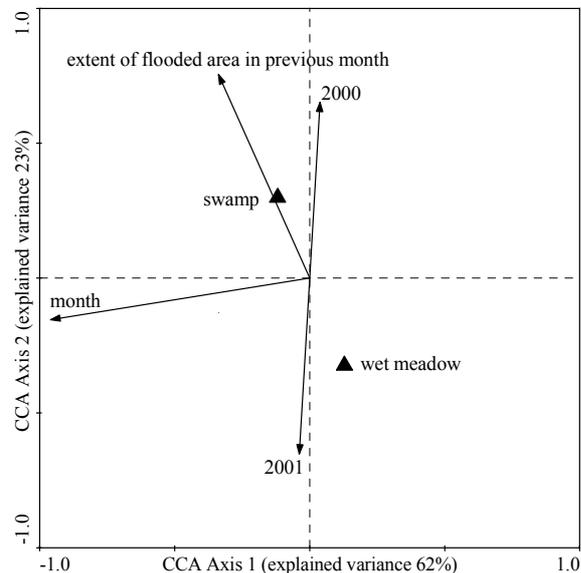
Figure 8. Ordination diagram based on canonical correspondence analysis of mosquito data from two years in four wetlands in the Nedre Dalälven region (data from two bogs is excluded in this analysis). Only the environmental variables are shown.

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breeding sites (Brust 1980). In 2000, its' population size was extremely high and it invaded more or less the whole region, including the bog Tavelmuren that is located approximately 14 km away from the River Dalälven. The percentage of similarity for mosquito assemblages was more than 70% for all wetlands regardless of distance and up to 90% between wetlands situated close to each other. In 2001, the population size of *Oc. sticticus* was smaller and accordingly the effect of distance was more distinct. The percentage of similarity in 2001 was lower than 50% for all wetlands located at a distance of at least 8 km from each other.

Permanence at local scale, shading at large spatial scale

Species diversity and community structures might be influenced by larger scales than the local habitat and the role of the surrounding landscape has been increasingly stressed (e.g. Kareiva and Wennergren 1995, Pickett and Cadenasso 1995, Miller et al. 1997). However, species perceive landscape structures at different spatial scales (Wiens 1989, Wiens and Milne 1989, Haslett 2001). Working with insects, it gets even more complicated because most insects have complex life cycles and use e.g. aquatic habitats as larvae and terrestrial habitats as adults. It was therefore interesting to include two insect families in this study, mosquitoes and diving beetles, that have complex life cycles and utilize both the aquatic and terrestrial part of wetlands. Focus was on the landscape variables permanence (proportion of permanent water bodies and temporary wetlands) and forest shading (proportion of forest and open land) since their influence on mosquito and diving beetles faunas is well documented (Bidlingmayer 1985, Becker 1989, Nilsson and Svensson 1995, Lundkvist et al. 2001, Lundkvist et al. 2002). The aim of the study was to evaluate the spatial scale of the influence of landscape variables on mosquito and diving beetle faunas. The hypothesis was that the expected effect of permanence and shading would be highest at the local scale and decrease with increasing distance in relation to the mobility of species.

   In line with the available information, most mosquito species preferred areas with high proportions of temporary wetlands (negative correlations with permanence indices) and high amounts of forest (positive correlations with shading indices) (Fig. 9). In accordance with the hypothesis, the importance of water permanence on mosquitoes was strongest at the local scale within 100 m around trap sites. This could be due to mosquitoes searching for an oviposition site or originating from the area. The influence of forest shading was however stronger at larger spatial scales which could be explained by dispersal behaviour. Most mosquito species have a flight range of several 100 to about 2,000 m (Jenkins and Hassett 1951, Nielsen 1957, Joslyn and Fish 1986, Schäfer et al. 1997) and thus were influenced by the shading indices within these distances. Some species such as *Ae. vexans* and
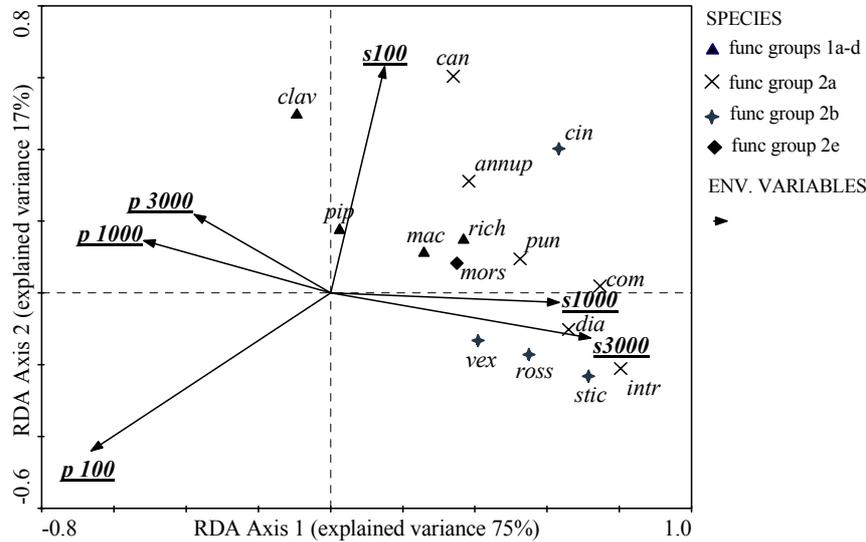
Figure 9. Mosquito species distribution in relation to the landscape variables permanence index (p) and shading index (s) at three spatial scales as determined by a redundancy analysis based on data from nine wetlands in southern and central Sweden. The most important variables are the proportion of temporary wetlands (negative correlations with p) within 100 m around trap sites, and the amount of forest (positive correlations with s) within 1000 and 3000 m around trap sites. Mosquitoes are sorted according to functional groups. Species abbreviation are explained in appendix 1, paper III. Species with less than 25 individuals in total are not shown in the diagram.

Oc. sticticus are however known for long-range dispersal and can fly at least 10 km from their breeding sites (Horsfall et al. 1973, Brust 1980). These species were mostly influenced by the shading index within 3,000 m around trap sites. The results showed that mosquito species were influenced by landscape variables at different spatial scales, depending mainly on their dispersal ability. This is in accordance with other studies (Keitt et al. 1997, With et al. 1999, Steffan-Dewenter et al. 2002).

Similar results were obtained for diving beetles (Fig. 10). They were mostly affected by water permanence at the local and intermediate scale (100 to 1,000 m around trap sites). This could indicate the activity radius of diving beetles searching for new habitat, food or oviposition sites. Species occurring in temporary habitats are generally good fliers with large range sizes while permanent habitats contain more diving beetle species without flight ability (Jackson 1952, Jackson 1956, Ribera and Vogler 2000). The influence of forest shading was also strongest at larger spatial scales (1,000-3,000 m).
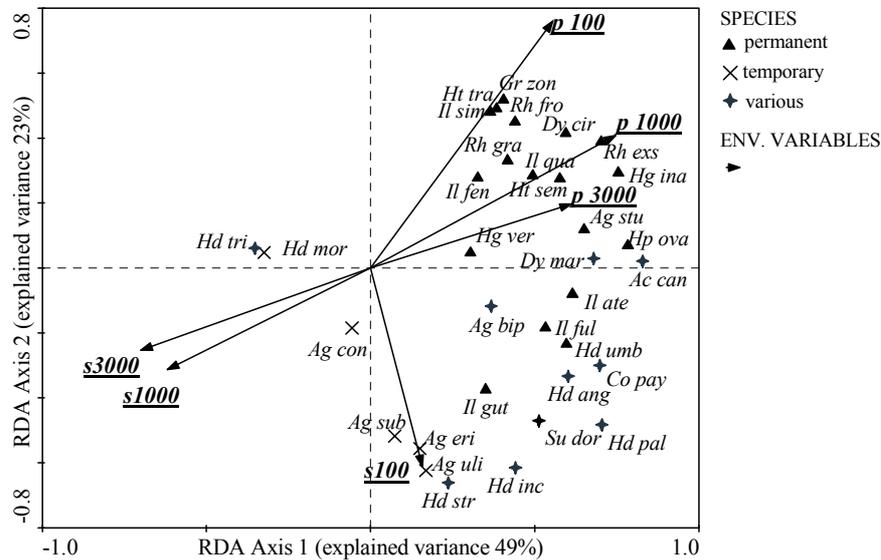
Figure 10. Dytiscid species distribution in relation to the landscape variables permanence index (p) and shading index (s) at three spatial scales as determined by a redundancy analysis based on data from nine wetlands in southern and central Sweden. The most important variables are the proportion of permanent water bodies (positive correlations with p) within 100 and 1000 m around trap sites, and the amount of open area (negative correlations with s) within 1000 and 3000 m around trap sites. Dytiscids are sorted according to preferred habitat type (permanent, temporary or various) following Nilsson and Holmen (1995). Species abbreviation are explained in appendix 2, paper III. Species with less than 20 individuals in total are not shown in the diagram.

Dispersing diving beetles are reported to be more attracted by open areas (Nilsson and Svensson 1995, Lundkvist et al. 2002). Unfortunately, not much is known about the flight range of individual diving beetle species. They are reported to disperse over a distance of several kilometres (Lundkvist et al. 2002), and the data from this study also suggests that some species could disperse distances of up to 3,000 m.

Wetland origin and size

Mosquito data from four natural and five constructed wetlands showed that adult mosquito assemblages differed between natural and constructed wetlands. In addition to ordination, I also employed a cluster analysis based on the Bray-Curtis similarity coefficient for quantitative data (Fig. 11). The nine wetlands formed three clusters with similar mosquito assemblages: one cluster with three natural wetlands, one cluster with three constructed and one natural wetland, and one cluster with two constructed wetlands. The natural

wetland STO (Stavsätter-old) that joined the cluster of three constructed wetlands was rather small and in addition affected by forestry activities. The two constructed wetlands SJN (Stjärnarp-new) and STN (Stavsätter-new) that formed a separate cluster were newly constructed wetlands and had only low mosquito numbers.

It is of special interest to find insect assemblages that discriminate between natural and constructed or restored wetlands. They could help in monitoring how insect communities in constructed wetlands develop over time and in comparison to natural wetlands. Streever at al. (1996) compared larval dipteran communities from natural and constructed wetlands but found no difference. On the other hand, D'Amico et al. (2004) report that adult dragonfly assemblages differed significantly between restored and reference shallow lakes. It is also important to consider the colonization ability of insects. Newly constructed wetlands are quickly colonized by certain taxa (including mosquitoes). Brown et al. (1997) compared macroinvertebrates of natural and restored wetlands during three years and found most taxa from natural wetlands also at the restored sites. My observed differences in mosquito assemblages of natural and constructed wetlands might partly be due to differences in wetland size between natural and constructed wetlands. In the redundancy analysis, wetland size alone explained 68% of the variation explained by all variables.
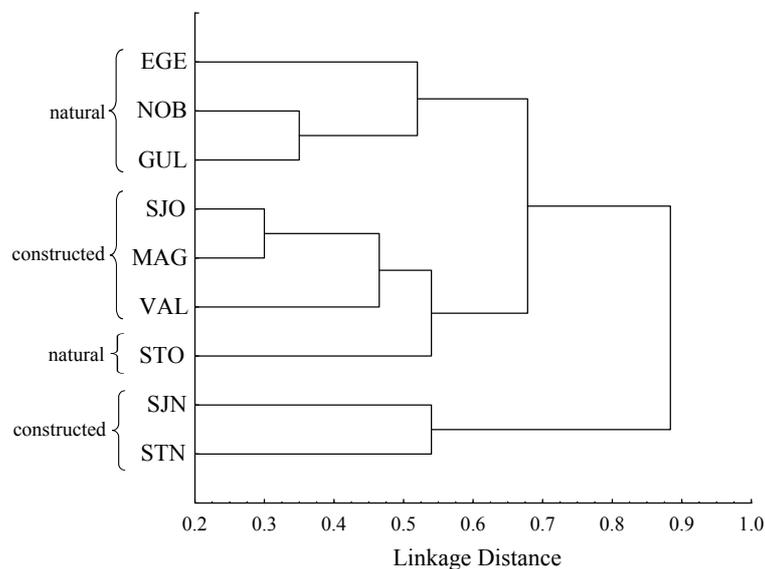
Figure 11. A cluster analysis based on the Bray-Curtis similarity coefficient for quantitative data for mosquito faunas from nine wetlands in Southern Sweden.

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Survival strategies of floodwater mosquito larvae

High numbers of adult mosquitoes provide evidence that they are extremely successful inhabitants of temporary wetlands. Becker et al. (2003) even claim that "respect is due to these tiny insects which have adapted their behaviour to overcome the hostile conditions in their breeding sites". Floodwater mosquito species show several adaptations for a life in temporary habitats. They produce drought-resistant eggs that can survive for several years and subsequent larval hatching needs to be triggered by several factors such as appropriate water temperature and a decline in dissolved oxygen. Larval development is temperature-dependent and can be completed within a short time frame. I investigated an additional potential adaptation of floodwater mosquito species to temporary wetlands, the responses of larvae to rapidly diminishing larval habitat. Models of complex life cycles predict that greater mortality at the immature stages should induce earlier metamorphosis at smaller sizes (Rowe and Ludwig 1991). This has been observed for the tree hole mosquito *Ochlerotatus triseriatus* in response to decreasing water volume (Juliano and Stoffregen 1994).

I experimentally tested the hypothesis that floodwater mosquitoes would respond to diminishing larval habitat by accelerating larval development time (paper V). Adults would emerge earlier but with smaller size. The species composition in the experiment, based on the emerged adults, was 87.9% *Ae. vexans* and 12.0% *Oc. sticticus*.
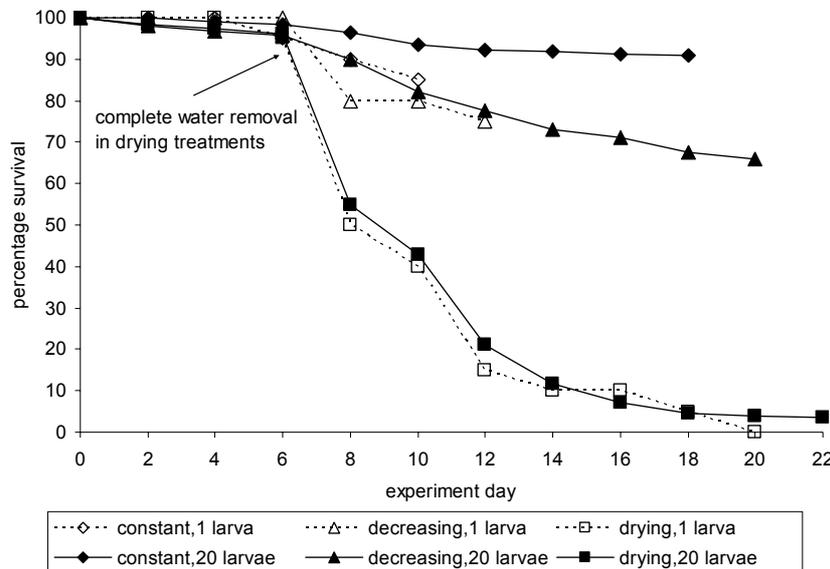
Figure 12. Percentage survival over time of floodwater mosquito species subject to three water level schedules and two larval densities.

Water level schedule had a significant effect on survival to adult emergence (Fig. 12). In the treatments with constant water level schedule, 91% of the mosquitoes survived to adults and in the decreasing water schedule 66% survived to adults. However, only 3% survived to adults in the drying treatments. Nevertheless, the last alive larva in these treatments was observed 14 days after water removal. The first adult from these treatments emerged six days after water removal and the last adult 14 days after water removal (all *Ae. vexans*).

In accordance with the hypothesis, *Oc. sticticus* adults emerged earlier in the decreasing than the constant water schedule (Fig. 13), but adult size was neither affected by water schedule nor by larval density. In contrast, time to emergence of *Ae. vexans* was significantly longer in the decreasing than the constant water schedule. Also, adults emerging from constant water schedule were larger than adults from decreasing water schedule. Larval density had no effect on time to emergence but adults emerging from containers with single larva were significantly larger than adults emerging from containers with 20 larvae.

These results indicate two survival strategies. *Oc. sticticus*, in accordance with the hypothesis, responded to diminishing habitat by accelerating larval development. *Ae. vexans*, however, showed remarkable survival ability in humid soil. Chodorowski (1969) commented on the ability of *Oc. communis* larvae to survive short (18 hours) waterless periods. He suggested that this ability might be more important for survival than an acceleration of development time. This might apply to *Ae. vexans* as well. A survival probability
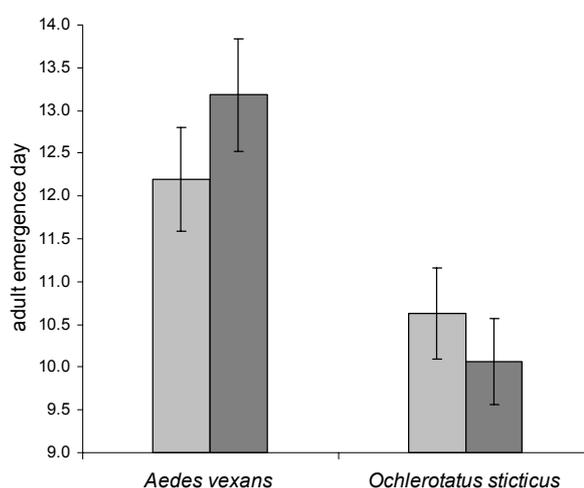
Figure 13. The effect of water schedule on mean time to adult emergence of *Ae. vexans* and *Oc. sticticus*. Light grey bars represent constant water schedule, dark grey bars represent decreasing water schedule.

of 3% would still result in large numbers of adult mosquitoes, considering the original number of larvae than can be found in temporary wetlands (e.g. approximately 10,000 *Ae. vexans* larvae per 1,000 ml in an inundation area in the Upper Rhine Valley, Germany, personal observation).

Ae. vexans and *Oc. sticticus* are two co-existing species in temporarily flooded areas and one of these two species is often predominating in inundation areas of large rivers. Adult sampling in the area where the larvae originated revealed *Oc. sticticus* to be the dominant species in the area, while *Ae. vexans* was the dominant species in the larval collections for the experiment. Maybe the natural conditions during June and July 2003 with a continuously decreasing water level of the River Dalälven favoured the species with fast development, *Oc. sticticus*, more than the one with the "sit-and-wait" strategy, *Ae. vexans*. This aspect also links this experimental study to the field studies on the effects of environmental variables on mosquito assemblages.

The results of this study could have some implications for mosquito control. Drying out of mosquito breeding sites is usually considered as making mosquito control unnecessary. However, my results indicate that drying out of a breeding site might not necessarily result in low adult mosquito population density. Since *Ae. vexans* has a high survival ability in humid soil, rainfall within 14 days after desiccation of wetlands could still enable adult mosquito hatching. Further experiments are needed to clarify the ability of different immature stages to survive waterless periods and to complete metamorphosis with adult emergence. It would also be desirable to test the response of mosquito species utilizing more permanent and stabile water bodies to diminishing larval habitat.

The problems with mosquitoes

Mosquitoes usually generate negative associations with nuisance and disease transmission. Therefore, I wanted to evaluate the risk of mosquito nuisance and disease transmission in constructed compared to natural wetlands, considering the fact that constructed wetlands are often situated close to human settlements and sometimes frequently visited by humans (paper IV). Mosquito abundance was higher in the natural than the constructed wetlands. But how to define and measure mosquito nuisance? According to Bradley and Travis (1943), a daily light trap catch of fewer than 25 individuals indicates that mosquitoes are not present in annoying numbers. With that definition, mosquito nuisance could be stated for seven of the nine wetlands in this study, including all four natural wetlands and three of the five constructed ones. However, one should remember that not all mosquito species are causing nuisance, and species with birds or amphibians as preferred blood meal hosts are not likely to cause trouble for humans. Most Swedish mosquito species show a preference for mammals, but then only those with the poten-

tial for mass-breeding during summer (functional group 2b), together with long distance dispersal ability, e.g. *Oc. sticticus* and *Ae. vexans*, should be considered major nuisance species. These two species were found in all constructed wetlands except for one (Stjärnarp-new). Their numbers were not sufficient to cause nuisance, but their presence nevertheless indicates a risk for massive production in the areas under certain conditions, i.e. increased summer rains. Of course other mosquitoes can be experienced as nuisance as well, but most species apart from those in functional group 2b present a nuisance only for a limited time period during summer. Species from functional group 2a (snow melt mosquitoes) are numerous all over Sweden during June but their numbers usually decline rapidly during July.

Substantial mosquito nuisance during the whole summer season caused by species in functional group 2b was experienced during the study in the Nedre Dalälven region (paper II). There, highest numbers of mosquitoes of all studies in this thesis were found and the species *Oc. sticticus* dominated the mosquito fauna. Variations in mosquito abundance could be attributed to the varying extent of flooding by the River Dalälven. Mosquito numbers varied significantly among years and among month of sampling (Fig. 14). Of the three wetland types included in this study, the swamps contained most mosquitoes followed by the wet meadows. In the bogs, mosquito numbers
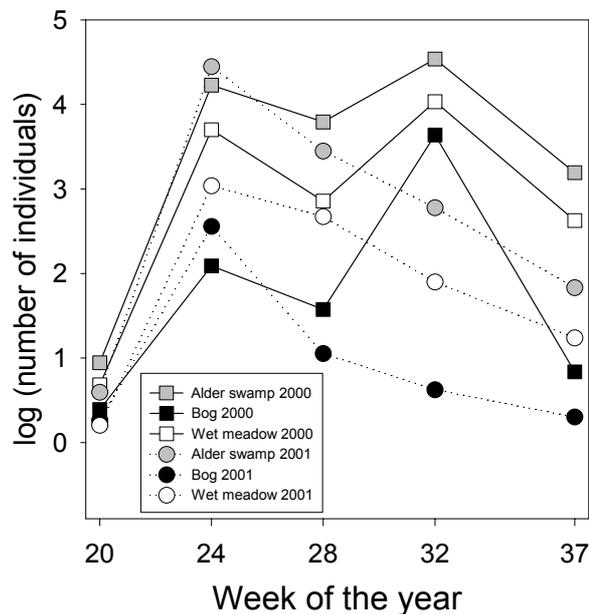
Figure 14. Variations in mosquito abundance in relation to wetland type, year of sampling and month of sampling, corrected for wetland size, based on collections in six wetlands in the Nedre Dalälven region, central Sweden, from May to September 2000 and 2001.

were lowest but they were nevertheless affected by adjacent inundated wetlands. Mosquito abundance was highest in August 2000 and I sampled approximately 62,100 mosquitoes in one CDC trap in the wet meadow Sälja during one night. These mosquito numbers were certainly experienced as annoying.

In addition to causing nuisance, mosquitoes cause problems by transmitting diseases. Therefore, collected mosquitoes were processed for virus isolation. In the Nedre Dalälven region, Sindbis virus has been isolated from *Ae. cinereus* collected close to Tärnsjö in 1995 and from *Ae. cinereus* collected close to Österfärnebo in 2000 (Lundström and Pfeffer, personal information). Besides, there was one human case of Ockelbo disease in Österfärnebo in 2002. Thus, there is a low but substantial risk of Sindbis virus transmission to humans by *Ae. cinereus* in the Nedre Dalälven region.

In the southern Swedish study areas (paper IV), no virus was found from a total of 36,247 mosquitoes collected in this study. However, Sindbis virus and other mosquito-borne zoonoses are known for a prevalence pattern characterized by several years of low activity followed by short bursts of activity resulting in local outbreaks and epidemics (Lundström et al. 1991, Lundström 1999). Thus, I also looked at the occurrence of *Cx. pipiens/torrentium* (enzootic vector) and *Ae. cinereus* (link vector). Their presence in the constructed wetlands indicate a low but significant risk that mosquito-borne bird viruses could establish their enzootic transmission cycles and also be transferred from birds to humans in populated areas. Three of the constructed wetlands were suitable for virus transmission to both birds and humans, and two of these wetlands, Magle and Vallås, present increased risk for transmission to humans because they were located close to human settlements and also frequently visited by humans.

Concluding remarks

Mosquitoes are hard-to-neglect inhabitants of wetland environments and part of the aims of this thesis was to assist a more genuine understanding of mosquito community structures from an ecological point of view. I could show that adult mosquito diversity and assemblages are influenced by a number of environmental variables such as wetland size, wetland type and surrounding landscape. In most previous studies, connections with environmental variables have been evaluated for eggs or larvae, and rarely for adult mosquitoes (Horsfall 1963, Cassani and Bland 1978, Sharkey et al. 1988, Wekesa et al. 1996). Studies about the spatial distribution of adult mosquitoes often consider single species that are important disease vectors (Wekesa et al. 1997, Gleiser et al. 2002). In this thesis, a more general approach was used.

Interestingly, the large periodically flooded wetlands had rather low mosquito diversity which was mainly due to high dominance of single species. Mosquito diversity was therefore positively influenced by an increased proportion of more permanent water bodies, as well as an increased amount of open areas. These features had a positive influence on dytiscid diversity as well, and might also promote diversity of other insects, e.g. dragonflies or caddis flies. When constructing wetlands with the aim to increase biodiversity, the landscape aspect should therefore be taken into consideration. High proportion of permanent water bodies and the "right" positioning in a landscape context could improve insect diversity. Placing a mainly permanent wetland in an open landscape could provide favourable conditions for both dytiscid and mosquito diversity, while at the same time reducing colonization by nuisance mosquito species (in particular species from functional groups 2a and b). Considering the importance of habitat heterogeneity, biodiversity could also be improved by a combination of several wetland types or subhabitats within a wetland, differing e.g. in hydroperiod, depth, vegetation, and type of substrates (Collinson et al. 1995, Wissinger 1999, Lundkvist et al. 2001).

Low production of major nuisance mosquito species might be crucial for acceptance of constructed or natural wetlands among human neighbours. In the U.S.A., recent discussions have taken up this topic, pointing out that abundant mosquito populations in constructed wetlands are not a surprising side effect, but rather a foreseeable effect of providing suitable habitat for them (Knight et al. 2003, Karpiscak et al. 2004, Willott 2004). Therefore, this problem should not be neglected but addressed, e.g. with wetland man-

agement and, if necessary, with mosquito control measurements. Monitoring of adult mosquitoes in constructed wetlands close to human settlements could help to detect and quantify the occurrence of potential nuisance species as well as potential vectors of disease. Such data enables a risk assessment and provides useful and important information in case mosquito control measurements would be needed.

An example of problems with human acceptance of wetlands due to mosquito nuisance can be found in the Färnebofjärden area in the Nedre Dalälven region. There, mosquitoes from inundated wetlands regularly invade human settlements located several kilometres from these wetlands. My collections in this region in 2000 coincided with tremendously high mosquito abundances and identified the major nuisance species. This documentation provided the basis for convincing both politicians and authorities that people in the villages Österfärnebo and Tärnsjö are subject to extreme mosquito annoyance and that mosquito control measurements are required to improve living conditions and general development in the region. Thus, initiated by the local people, the project "Biologisk Myggkontroll Nedre Dalälven" (Biological Mosquito Control Nedre Dalälven) was started in the same year with the goal to reduce numbers of floodwater mosquitoes to a more acceptable level. Since 2002, regular mosquito control is conducted by applying the larvicide *Bacillus thuringiensis israelensis* (BTI) by helicopter to mosquito breeding sites. Hopefully, this has helped to turn the rather negative feelings against wetlands to a more positive appreciation of the unique nature in this region.

Acknowledgements

"En jägare som jagar myggor fäller ingen älg…"
…men kan nog "fälla" en avhandling till sist.

(a hunter who hunts mosquitoes does not bring down a moose…)

"Bringing down" this thesis would not have been possible without the help and support of colleagues, friends and family.

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Martina

Sammanfattning

Våtmarker innehåller såväl akvatiska som terrestra miljöer, vilket generellt inducerar en hög biologisk mångfald (biodiversitet). Begreppet biodiversitet inkluderar alla livsformer, även sådana som av människor kan uppfattas som besvärande eller obehagliga. Stickmyggor är en del av våtmarkernas biodiversitet, men de anses vanligen som negativa, dels för att honor av flertalet arter angriper och tar blod från människor, dels för att några arter av stickmyggor sprider infektioner. Min avhandling syftar till att klarlägga sambanden mellan våtmarker och stickmyggor i Sverige. Mönster hos den vuxna stickmyggfaunans diversitet studerades initialt med fokus på en nord-sydlig gradient över hela landet och övergick sedan till mer detaljerade studier i södra och centrala Sverige. I centrala Sverige i området vid Nedre Dalälven undersökte jag betydelsen av våtmarkernas typ (sumpskog, fuktäng, mosse) och storlek, avstånd mellan studieområden samt tidsaspekter på översvämningar. I centrala och södra Sverige studerades betydelsen av våtmarkernas och den omgivande miljöns struktur, i form av öppna och beskogade ytor respektive vattenytor av kort och lång varaktighet, för såväl stickmyggor som dykarskalbaggar. Dessutom gjordes en detaljerad studie av stickmyggfaunans komposition i naturliga och konstruerade våtmarker i södra Sverige. Experimentellt undersökte jag hur snabb uttorkning av den akvatiska miljön påverkar utvecklingen från larv till vuxen mygga hos två arter översvämningsmyggor.

Inventeringar av vuxna stickmyggor genomfördes inom 18 våtmarker fördelade över hela landet med hjälp av standardiserade myggfällor och insamlingarna utfördes över hela sommaren. Svenska stickmyggor organiserades i tio funktionella grupper baserande på fyra kriteria: 1) substrat för äggläggning (på vatten eller fuktig mark), 2) övervintrade stadium (ägg, larv eller vuxen hona), 3) viktigaste grupp av värddjur för blodsugning (däggdjur inklusive människor, fåglar eller grodor), och 4) antal generationer per år (en eller flera). De funktionella grupperna användes dels som komplement till andra mått på stickmyggfaunans diversitet, dels för mer mottagarvänlig presentation av resultat från undersökningar av myggfaunan. De tio funktionella grupper visade en geografisk variation från två funktionella grupper i norra, över sju i centrala till nio i södra delen av landet. Vid jämförelser mellan våtmarker i ett mer regionalt perspektiv var dock urskiljningsgraden relativt låg. Simultana analyser av myggfaunans komposition och abundans per art visade dock att arter inom samma funktionella grupp även grupperade sig

avseende ett antal miljövariabler, vilket visar att de funktionella grupperna har en biologisk relevans.

Diversitet hos svenska stickmyggor visade flera välkända och för andra organismer redan etablerade mönster: ökande diversitet från norr till söder, positivt samband mellan antal arter och storlek på områden, arter som förekom i stort antal fanns också i många områden. Mina resultat visade dessutom att diversitet hos stickmygg och dykarskalbaggar samvarierade i ett landskapsperspektiv och att hög diversitet hos båda dessa insektfamiljer relaterar till miljöer med hög andel permanent vatten och omgivna av öppen mark

Stickmyggfaunans komposition och arternas inbördes abundansförhållanden i våtmarkerna kring Nedre Dalälven styrs främst av översvämningarnas periodicitet och omfattning men även av våtmarkstyp. Mycket hög abundans av stickmyggor kan kopplas till stora våtmarker med återkommande översvämningar sommartid. Stickmyggfaunan i dessa våtmarker dominerades kraftigt av en art vilket medförde högt dominansindex och därför lågt diversitetsindex. Andelen temporära våtmarker har stor betydelse för stickmyggfaunan i ett lokalt perspektiv, men i ett större landskapsperspektiv får andelen skogsmark en ökande betydelse eftersom stickmyggornas spridningsbeteende kommer in i bilden. I Södra Sverige skilde sig stickmyggfaunorna mellan naturliga och anlagda våtmarker och både antal arter och antal individer var lägre i anlagda än i naturliga våtmarker.

I mitt experiment kunde jag visa att två arter översvämningsmyggor reagerar på olika sätt vid snabb uttorkning av deras larvmiljö. Den ena arten visade snabbare larvutveckling med tidigare kläckning av vuxna myggor i minskande vattennivå jämfört med konstant vattennivå. Den andra arten visade en annan strategi. Larvarna överlevde i fuktig mark upp till 14 dagar och en viss del lyckades fullborda utvecklingen till vuxna stickmyggor. Detta indikerar att väderförhållande efter en översvämning kan påverka stickmyggfaunans komposition, samt att uttorkning av våtmarker inte nödvändigtvis stoppar produktionen av vuxna mygg.

Mina resultat innehåller förslag till konstruktion och miljömässig positionering av konstruerade våtmarker för att uppnå en balans mellan hög diversitet hos både stickmyggor och dykarskalbaggar samt en låg abundans av de arter stickmyggor som orsakar mer betydande problem. Generell sett kan låg abundans av dessa arter stickmyggor ha en avgörande betydelse för samhällets acceptans av tätortsnära våtmarksområden.

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Zusammenfassung

Meine Doktorarbeit befasst sich mit Feuchtgebieten, Stechmücken („Schnaken") und ihrer biologischen Vielfalt („Biodiversität"). Das Hauptziel war besser zu verstehen, welche Umweltfaktoren die Stechmückenfauna eines Gebiets beeinflussen. Teilarbeiten befassten sich mit: a) Feuchtgebiete in einem Gradient von Nord- nach Südschweden; b) drei Arten von Feuchtgebieten (Feuchtwiese, Erlenwald und Moor) im Gebiet „Nedre Dalälven" in Mittelschweden; c) die landschaftliche Beschaffenheit der Umgebung von Feuchtgebieten in Süd- und Mittelschweden (in dieser Untersuchung wurden auch Schwimmkäfer, Dytiscidae, erfasst); d) ein Vergleich von natürlichen und künstlich angelegten Feuchtgebieten in Südschweden; und e) eine experimentelle Untersuchung, wie die Larven zweier Arten Überschwemmungsmücken auf das Austrocknen ihres Lebensraums reagieren.

Die Stechmückenfauna wurde in allen Feldstudien mit Standardfallen erfasst, wobei in der Regel drei Fallen pro Untersuchungsgebiet über drei Nächte pro Monat von Mai bis September im Einsatz waren. Die Larven für das Experiment wurden in Überschwemmungsgebieten in der Nähe von Österfärnebo gesammelt.

Ich teilte die 47 in Schweden vorkommenden Stechmückenarten in zehn funktionelle Gruppen ein. Die Einteilung beruhte auf folgenden Kriterien: wo werden die Eier abgelegt (Wasser oder Land), welches Stadium überwintert (Ei, Larve oder Weibchen), welche Tiergruppe wird bevorzugt gestochen (Säugetiere inklusive Mensch, Vögel oder Amphibien) und wie viele Generationen gibt es pro Saison (eine oder mehrere). Die funktionellen Gruppen erwiesen sich sowohl beim Auswerten der Ergebnisse als auch bei Vorträgen nützlich.

Sowohl die Anzahl der Stechmückenarten als auch die Anzahl der funktionellen Gruppen nahm von Nord- nach Südschweden zu. Ein solcher Gradient entspricht einem allgemeinen ökologischen Muster, das man auch für andere Tiergruppen gefunden hat.

In der Untersuchung im Gebiet „Nedre Dalälven" unterschied sich die Stechmückenfauna in den drei verschiedenen Feuchtgebieten. Die Feuchtwiesen und Erlenwälder waren außerdem direkt vom Wasserregime des Flusses Dalälven beeinflusst. Das Ausmaß der überschwemmten Flächen in den Untersuchungsgebieten wurde mittels eines digitalen Terrainmodels berechnet. Durch die Schwankungen in diesen Flächen während einer Saison konnte ein Grossteil der Variation in der Stechmückenfauna erklärt werden.

Die Anzahl der Stechmücken in diesem Gebiet war extrem hoch, und die höchsten Werte wurden im August 2000 erreicht. In einer Falle auf einer Feuchtwiese fing ich ungefähr 62100 Stechmücken in nur einer Nacht. Die Fänge waren außerdem stark dominiert von einer Art, der Überschwemmungsmücke *Ochlerotatus sticticus.*

Die landschaftliche Beschaffenheit rund um ein Feuchtgebiet hat ebenfalls Einfluss auf die Stechmückenfauna. In dieser Untersuchung beschränkte ich mich auf zwei Landschaftsfaktoren, dem Anteil an Dauergewässern im Verhältnis zu temporären Gewässern (Tümpel) und dem Anteil an Wald im Verhältnis zu offenen Flächen. Die Bedeutung dieser Faktoren wurde mit zunehmendem Abstand (bis 3000 m) vom Feuchtgebiet ausgewertet. Die Gewässerdauer ist hauptsächlich im Feuchtgebiet selbst von Bedeutung, während der Waldanteil mit zunehmendem Abstand an Bedeutung gewinnt. Hier spielt das Wanderverhalten der Stechmücken eine Rolle. Für die meisten Arten ist der Waldanteil bis zu einer Entfernung von 1000 bis 2000 m vom Feuchtgebiet wichtig, und dies entspricht der Entfernung, die diese Arten durchschnittlich fliegen. Schwimmkäfer zeigten ein ähnliches Verhalten. Leider weiß man nur wenig über die Entfernungen, die Schwimmkäfer fliegen. Meine Ergebnisse deuten darauf hin, dass sich die meisten flugfähigen Schwimmkäfer in einem Radius von 3000 m bewegen. In dieser Untersuchung zeigte sich außerdem, dass die Diversität von sowohl Stechmücken als auch Schwimmkäfern positiv von den gleichen Landschaftsstrukturen (hoher Anteil permanenter Gewässer und offener Landschaft) beeinflusst wird. Damit könnten neu angelegte Feuchtgebiete so in die Landschaft angepasst werden, dass eine hohe Insektendiversität gefördert wird, während gleichzeitig die Ansiedlung plageerregender Stechmückenarten erschwert wird.

Die Stechmückenfaunen von natürlichen und künstlich angelegten Feuchtgebieten unterschieden sich deutlich. In den natürlichen Feuchtgebieten war sowohl die Anzahl der Stechmücken als auch die Anzahl der Arten höher als in den angelegten. Typische plageerregende Stechmückenarten mit Massenvorkommen und ausgeprägtem Wanderverhalten (z.B. *Ochlerotatus sticticus* oder *Aedes vexans)* waren seltener in den angelegten als in den natürlichen Untersuchungsgebieten. Ihr generelles Vorkommen deutet jedoch darauf hin, dass veränderte klimatische Bedingungen (regenreiche Sommer) zu einem verstärkten Auftreten dieser Arten führen können.

In dem Experiment über die Reaktion von Stechmückenlarven auf das Austrocknen ihres Lebensraums wurden zwei Arten getestet, die oft zusammen in Überschwemmungsgebieten vorkommen, wobei meistens eine der zwei Arten dominiert. Die beiden Stechmückenarten zeigten unterschiedliche Reaktionen. Die Art *Ochlerotatus sticticus* beschleunigte die Larvenentwicklung mit abnehmendem Wasserstand im Vergleich zu konstantem Wasserstand, und das voll entwickelte Insekt schlüpfte früher. Die Art *Aedes vexans* zeigte mehr eine „Abwarten-Strategie". Abnehmender Wasserstand

setzte keine Beschleunigung der Larvenentwicklung in Gang, doch war die Überlebensrate und Überlebensdauer in den ausgetrockneten Versuchsbehältern unerwartet hoch. Die voll entwickelten Stechmücken schlüpften sechs bis 14 Tage nach dem kompletten Austrocknen und 3% der ursprünglichen Larvenanzahl überlebten ins Erwachsenenstadium. Die Ergebnisse weisen darauf hin, dass die klimatischen Bedingungen nach einer Überschwemmung eine der beiden Arten begünstigen könnte. In den Larveneinsammlungen für das Experiment dominierte *Aedes vexans* während Fallenfänge der Fluginsekten in dem Ursprungsgebiet der Larven von *Ochlerotatus sticticus* dominiert waren. Der Wasserstand des Dalälven ging schnell und kontinuierlich zurück nach dem Hochwasser und in diesem Fall erscheint die Strategie von *Ochlerotatus sticticus* erfolgreicher als die von *Aedes vexans.*

Feuchtgebiete sind nach wie vor bedrohte Lebensräume, auch wenn sie in zunehmendem Maße geschützt oder auch restauriert und neu angelegt werden. Diesen positiven Trend gilt es zu fördern, und dabei kann das Massenvorkommen von Stechmücken einen Rückschlag bedeuten. Die Akzeptanz von Feuchtgebieten in der Bevölkerung ist zu einem Grossteil davon abhängig, dass die Stechmücken nicht zur Plage werden. Daher ist es wichtig, dieses Problem nicht unter den Tisch zu kehren. Als Beispiel sei das Gebiet rund um den Färnebofjärden am Dalälven genannt. Hier erzeugen regelmäßig vorkommende Stechmückenplagen in den umliegenden Ortschaften eine negative Einstellung der Bevölkerung zu Feuchtgebieten. In meiner Untersuchung konnte ich enorm hohe Stechmückenzahlen und auch den Verursacher der Stechmückenplage, *Ochlerotatus sticticus,* dokumentieren. Diese Dokumentation diente als Grundlage eines Antrags, der Politiker und Behörden von der Notwendigkeit einer Stechmückenbekämpfung auf Begehren der Bewohner Österfärnebos und Tärnsjös überzeugte. Damit konnte diese Arbeit dazu beitragen, das Projekt „Biologische Stechmückenbekämpfung Nedre Dalälven" ins Leben zu rufen. Es steht zu hoffen, dass damit die negative Einstellung zu Feuchtgebieten in eine positivere Wertschätzung der einzigartigen Natur im Färnebofjärden umgewandelt werden konnte.

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