

# Systematic and Biogeographical Account of the Midges and Flies (Diptera) of the East Frisian Islands<sup>1</sup>

(Die Mücken und Fliegen der Ostfriesischen Inseln)

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## 1 Introduction

Biogeographical island research in North-West Germany has two roots:

- Since the middle of the 19th century the question of species richness on islands is discussed. From the approaches by Wallace and Darwin the conclusion was drawn that island fauna and flora is comparably poor in species

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<sup>1</sup>) Printed draft of an oral presentation on April, 21<sup>st</sup> 2009 at BTU Cottbus.

numbers, and early ecologists tried to reject that hypothesis by means of empirical data.

- During the 19th century a broad natural history research in various regions were carried out, including inventarization of the occurring plant and animal species of various regions ("Heimatsforschung"), including the Frisian Islands.

Zoological research started with Oskar Schneider in the late 19th century; he systematically investigated the fauna of Borkum. During the last 100 years, various studies on the island flora and fauna were carried out.

Subsequently, Dietrich Alfken investigated the small young islands Mellum and Memmert, Friedrich and Richard Struve continued the faunistic inventarization on Borkum from 1932 to 1946.

Later, since ca. 1975, the research on old and young East Frisian Islands has been broadly extended. - Intermediate results have been published subsequently; in 1993 a first compilation was given (Bröring et al. 1993).

Objectives of the scientific research during the investigations within the past 30 years on the islands were:

- Specification of characteristic features and properties of the island fauna and flora in total, and analysis of species assemblages of various coastal biotopes under protection, like sandy dune areas and salt marshes.
- Description and explanation of species area, and species abundance relations, respectively, contribution to theory of island biogeography.

The **Blue Book** (Niedringhaus et al. 2008) comprises catalogues of all plants and animals known from the East Frisian Islands to date (2008), including information on distribution, abundance and general biology of occurring species. The basis for the compilation is an inventarization from 1975 to 2005, and literature review. More than 50 authors contributed. Five chapters deal with the distribution and abundance of Flies and Midges (Diptera) on the islands. Some results were also published on the internet (<http://www.natosti.uni-oldenburg.de/>).

## 2 Methods and Geographical Remarks

Procedure and methods of scientific research include inventarization of all plants and animals of the East Frisian Islands as well as the reconstruction of the colonization process by including all sampling results since the beginning of the scientific research (literature review since ca. 1850), and by revision of old collections. Special reference was laid on the young islands Memmert and Mellum, which are about 150 years old, and where the colonization process could be studied directly.

In many cases it was necessary to solve difficult taxonomic problems, as often for old specifications in old papers no specimen for reaudit are available. The following example might be an illustration:

Schneider (1898) listed a Muscid (!) *Siphona flavifrons* (Zetterstedt) for Spiekeroog, it was based on investigations by Hess (1881) and Poppe (1891). However, genus *Siphona* is not a genus of Muscidae but a Tachinidae, and in Tachinidae no taxon „*flavifrons* Zetterstedt“ exists.

I. Solving the Problem: There is a *flavifrons* (Zetterstedt) in the genus *Delia*, however, this is an Anthomyiidae. As Muscidae and Anthomyiidae can easily be mismatched (most likely in the 19th century!), possibly, the Anthomyiidae *Delia flavifrons* (Zetterstedt) is meant. According to Adaschkiewitz (2007, in lit.) this species has been synonymized to *Delia pruinosa* (Zetterstedt), and that would mean that this species had been found on Spiekeroog.

II. Solving the Problem: In Tachinidae we have the species *Siphona flavifrons* (Staeger), however, it was never found elsewhere on the islands, but *Siphona cristata* (F.) and *S. geniculata* (DeGeer) instead. Possibly, it was an error in assigning correct taxonomy, or a wrong determination.

I decided to include *Siphona flavifrons* (Staeger) in the list of species.

An overview of the various important data of the nine islands Borkum, Juist, Norderney, Baltrum, Langeoog, Spiekeroog, Wangeroge, and the young islands Memmert and Mellum in front of the North West german coast is given in Table 1. Area size ranges from app. 40 sqkm to app. 7 sqkm for the old islands. It is important to realize that the number of inhabitants strongly varies, and up to app. 3 million accomodations of tourists are registered. A geographical outline of the North german coast with the wadden sea area is given in figure 1.

Table 1: East Frisian Island Archipelago (data according to Niedringhaus et al. [eds.] 2008); Bo = Borkum, Mt = Memmert, Ju = Juist, No = Norderney, Ba = Baltrum, La = Langeoog, Sp = Spiekeroog, Wa = Wangerooge, Me = Mellum; Area Size in qkm, Distance to Mainland (ML) in km; Heterogeneity: Shannon-Entropy based on the area size of classified habitat types; inhabitants in 2005, accomodations in thousands per year (data for 1994).

	<b>Bo</b>	<b>Mt</b>	<b>Ju</b>	<b>No</b>	<b>Ba</b>	<b>La</b>	<b>Sp</b>	<b>Wa</b>	<b>Me</b>
Area Size	38.9	4.3	18.3	27.6	7.1	22.4	20.4	9.8	4.9
Distance to ML	10.5	13.0	8.0	3.0	4.5	5.0	6.5	6.5	6.0
Plant Species	655	177	527	641	454	550	451	516	185
Animal Species	4996	2460	1908	2698	1160	2154	2108	1961	2267
Heterogeneity	2.23	1.17	2.20	2.24	2.00	2.37	1.96	2.14	1.02
Inhabitants	5900	-	1800	6200	500	2000	800	970	-
Accomodations	2249	-	921	2939	495	1473	580	896	-



Fig. 1: North-west German shoreline and the German Wadden Sea islands in the southern North Sea area.

### 3 Arthropoda Diptera: General Systematic Account

Arthropoda Diptera is an order of holometabolous Insecta: Pterygota (Insects with wings). It comprises species with reduced hind wings, balancers (halteres), including the midges and the true flies. About 150,000 species are described, in Central Europe a few more than 10,000 species, and in Germany some 9,500 species (100 families) occur. There is an extremely huge variability within and among the various groups and families of Diptera, as to morphological features, occurrence, feeding, and ethology.

#### Diagnostic Features of Main Systematic Units in Order Diptera

- Midges and True Flies with "balancers" (halteres, "Schwingkölbchen"), i.e. reduced hind wings.
- **Midges** (Nematocera) with filamentous, multi-segmented long antennae, **True Flies** (Brachycera) with short antennae which consist of different shaped segments.

- **True Flies** are divided into
  - cleft eclosing flies (Orthorrhapha, “Spaltschlüfer”), without horseshoe-shaped fissure (ptilinal suture) at the head,
  - cap eclosing flies (Cyclorrhapha, “Deckelschlüfer”), with horseshoe-shaped fissure (ptilinal suture) at the head.

## Diagnostic Features of Main Systematic Units in Order Diptera Brachycera

By application of the classification according to the eclosing strategy four groups can be divided:

- Orthorrhapha (cleft eclosing flies, “Spaltschlüfer”), without horseshoe-shaped fissure (ptilinal suture) at the head.
- Cyclorrhapha Aschiza (cap eclosing flies, “Deckelschlüfer”), with horseshoe-shaped fissure (ptilinal suture) at the head, and without inflatable membraneous sac in front of the head.
- Cyclorrhapha Schizophora Acalyptratae (cap eclosing flies, “Deckelschlüfer”), with horseshoe-shaped fissure (ptilinal suture) at the head, and with inflatable membraneous sac in front of the head (Ptilinum).
- Cyclorrhapha Schizophora Calyptratae (cap eclosing flies, “Deckelschlüfer”), with horseshoe-shaped fissure (ptilinal suture) at the head, and with inflatable membraneous sac in front of the head (Ptilinum), and with large wing flaps extending the halteres (“Calypters”, “Landeklappen”).

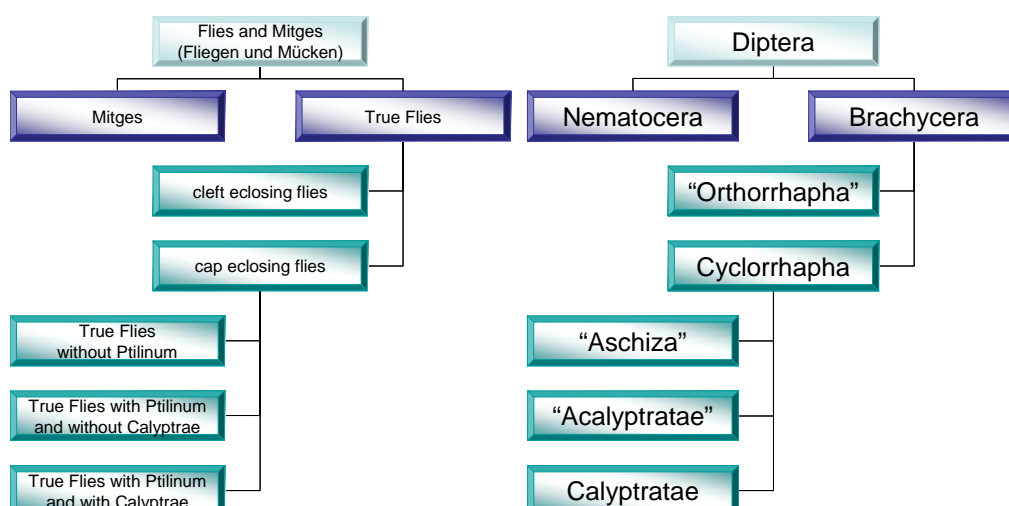


Fig. 2: Overview on the systematics of Diptera (quotation-marks denote non-monophyletic taxa, the status of Nematocera is still discussed).

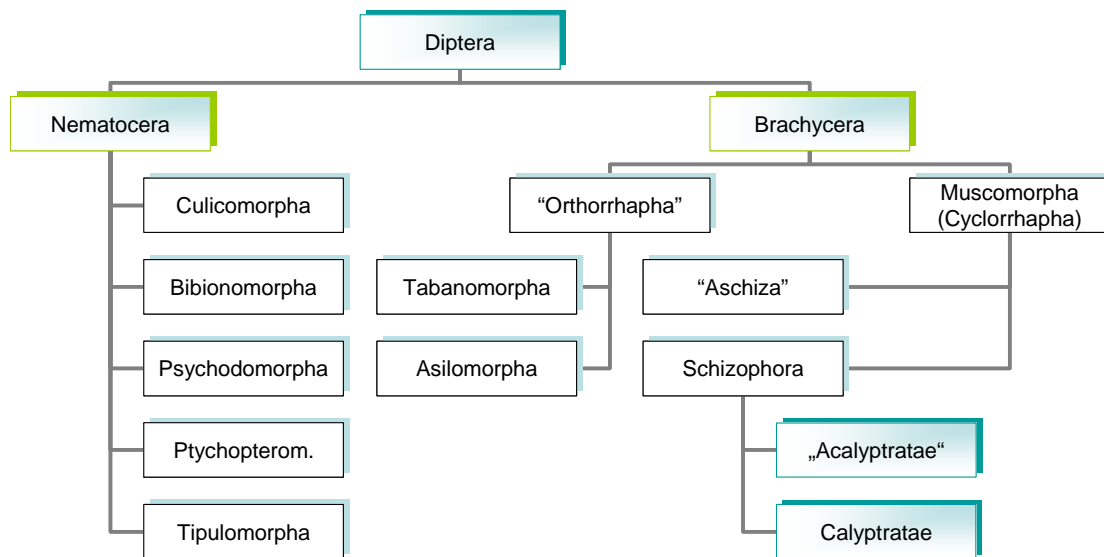


Fig. 3: Systematics of Diptera, new classification (quotation-marks indicate non-monophyletic taxa, the status of Nematocera and some infraorders within Nematocera are still discussed).

## 4 Arthropoda Diptera: Occurrence on Wadden Sea Islands

Various scientific questions have been addressed:

- How many species of Diptera are there on the wadden sea islands?
- What about the reliability of data on species numbers on the islands?
- Are there any significant differences to other groups of animals, and if so, what are the reasons?
- Are there any endangered species or species restricted to island or coastal sites on the islands?
- What about the colonization of different sites and habitats on the islands, such as dune areas and salt marshes?
- What about the colonization process on the islands: is there any increase or decrease of the species numbers on the islands (or equilibrium?) and what is the reason for such diversification, biodiversity loss?
- Is there any change in the species composition (huge species turnover)?

The following tables comprise an overview on the species numbers of the various groups of Diptera in relation to the German species numbers in total (tab. 2) and a comparison of the colonization rate for various arthropod groups expressed by the relation to species number in Lower Saxony and Germany in total (tab. 3).

Table 2: Species numbers of various groups of Diptera on the East Frisian Islands compared to species numbers of Germany (data according to Niedringhaus et al. 2008).

Group	Authors	Island Fauna	Germany	Relation
Nematocera	Niedringhaus	195	3800	5 %
Orthorrh. I.	Bröring & Niedringhaus	45	340	13 %
Orthorrh. II.	Meyer & Schleppegrell	177	1060	17 %
"Aschiza"	Bröring	124	950	12 %
Acalyptrata	von Tschirnhaus	515	1930	27 %
Calypttrata	Bröring	280	1400	20 %
<b>Diptera (total)</b>		<b>1336</b>	<b>9350</b>	<b>14 %</b>

Table 3: Colonization rate of Diptera compared to other animals (Auchenorrhyncha, Hymenoptera „Aculeata“, Heteroptera, Hymenoptera Symphyta, Heteroptera Nepomorpha et Gerromorpha, and Diptera considered; data according to Niedringhaus et al. 2008; \*) = rough estimation).

Group	Proportion Germany	Proportion Lower Saxony
Leafhoppers	31 %	43 %
Bees / Wasps	27 %	49 %
Bugs	29 %	39 %
Sawflies	30 %	47 %
Water Bugs	67 %	72 %
<b>Midges / Flies</b>	<b>14 %</b>	<b>20 %*)</b>
<b>Animal Species (tot.)</b>	<b>30 %*)</b>	<b>40 %*)</b>

The following results can be drawn:

- The colonization success of various groups of Diptera seems to be different, however, the variation of the compiled relations to species numbers in Germany are partly due to differing investigation efforts.
- The investigation of the Diptera-Fauna is rather insufficient, as further investigations will lead to an enormous increase of species numbers; roughly estimated, half of the occurring island species are listed to date.

Table 4: Species Numbers of Diptera on the East Frisian Islands (Bo = Borkum, Mt = Memmert, Ju = Juist, No = Norderney, Ba = Baltrum, La = Langeoog, Sp = Spiekeroog, Wa = Wangerooge, Me = Mellum; data according to Niedringhaus et al. 2008).

<b>Group</b>	<b>Bo</b>	<b>Mt</b>	<b>Ju</b>	<b>No</b>	<b>Ba</b>	<b>La</b>	<b>Sp</b>	<b>Wa</b>	<b>Me</b>
Nematocera	100	82	16	26	-	12	17	2	70
Orthorrh. I.	38	25	16	14	6	6	4	8	13
Orthorrh. II	131	46	17	38	-	4	18	30	85
„Aschiza“	87	57	43	53	19	48	37	45	45
Acalyptratae	220	270	77	80	15	22	94	11	271
Calypttratae	213	122	59	58	-	17	73	5	55
<b>Diptera (total)</b>	<b>789</b>	<b>602</b>	<b>228</b>	<b>269</b>	<b>40</b>	<b>109</b>	<b>243</b>	<b>101</b>	<b>539</b>

## Endangered Species

Reliable information is available only for two groups:

Orthorrhapha: Syrphidae (Hoverflies)

At least 13 species endangered (according to RL Germany) which is 12.4 % of all species found on the islands (for details see Bröring 2008).

Orthorrhapha: Empididae et Dolichopodidae (Long Legged Flies and Dance Flies)

At least 28 species endangered (according to RL Germany) which is 15.8 % of all species found on the islands (for details see Meyer & Schleppegrell 2008).

For other diptera families no up to date Red List is available.

## Colonization of Various Habitats on the Islands

Various habitats can be classified on the islands roughly (see for examples fig. 4 and 5):

- Xeroseries: sandy dune areas
- Haloseries: various salt marshes
- Hygroseries: more or less damp to wet habitats in dune areas
- Anthropogenous habitats (planted trees, urban areas, gardens)
- Aquatic environments and shorelines



Fig. 4: Various island habitats, including grey dune area (Norderney, Aug. 2008, Foto B. Bröring).



Fig. 5: Young dune and white dune area (Norderney, Aug. 2008)

Each of the classified habitats is colonized by diptera species (of course, parasitic species occur where hosts live). The colonization of the various habitats by diptera species can be exemplified in detail for the families Empididae and Dolichopodidae (dance flies and long legged flies, fig. 6). In total, 177 species were found on the islands to date. Note that about  $\frac{1}{4}$  of all species of these families occur within the shore area, however, in all classified sites a reasonable number of species occur.

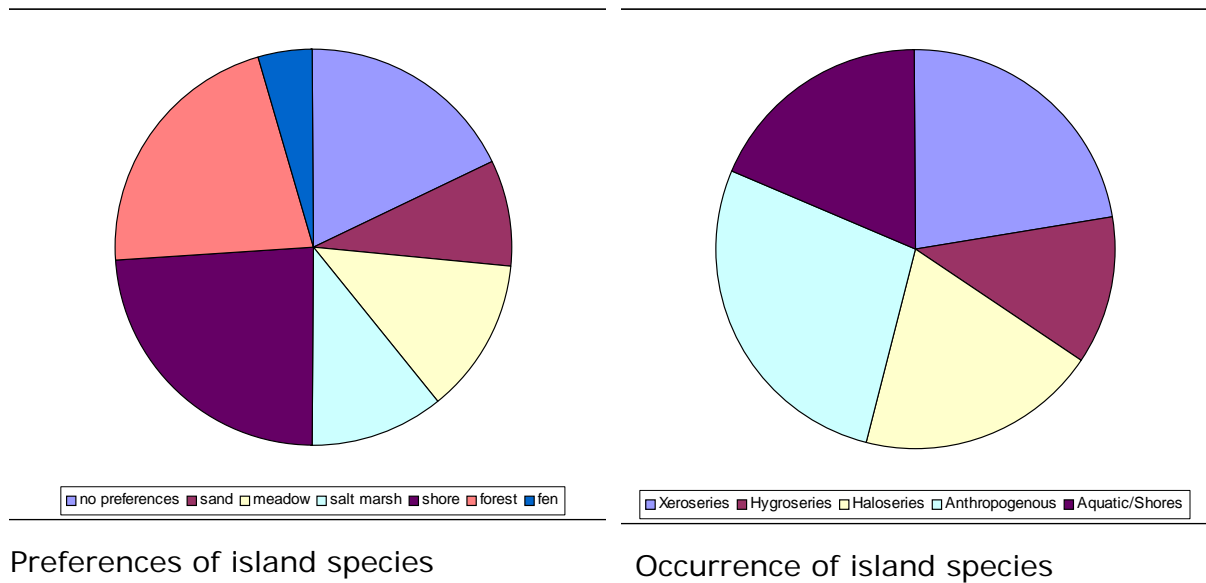


Fig. 6: Colonization of various habitats by long legged flies and dance flies (Dolichopodidae, Empididae, data according to Meyer & Schleppegrell 2008).

## 5 Biogeography: Species-Area-Relations

Within the framework of a biogeographical analysis the relation between species number and area size is analyzed. The question to be answered is: Are there more species on larger islands, and does the equation hold: The larger the island area, the higher the number of species. However, often a significant relation was found between species number and habitat heterogeneity. Further questions are: What about "habitat within - and "habitat between - correlations" to species numbers? What about the impact of human population density on species numbers, as human activities often lead to diversification of habitats.

Many Diptera-Species occur in or near villages and urban areas, resp. (e.g. house flies, window flies, cabbage flies), so that the number of island inhabitants might be an indicator for the diversity of diptera fauna.

### Analysis of Species Numbers: Results

Reliable data as to the analysis of species area relations are available only for one of the included diptera-families, the hoverflies (Syrphidae). The correlation is slightly significant for the Syrphidae ( $R = 0.64$ ,  $p < 0.05$ ), presumably, a stronger relation will be found when all groups of diptera are included. By using the present data no significant correlation could be detected (fig. 7).

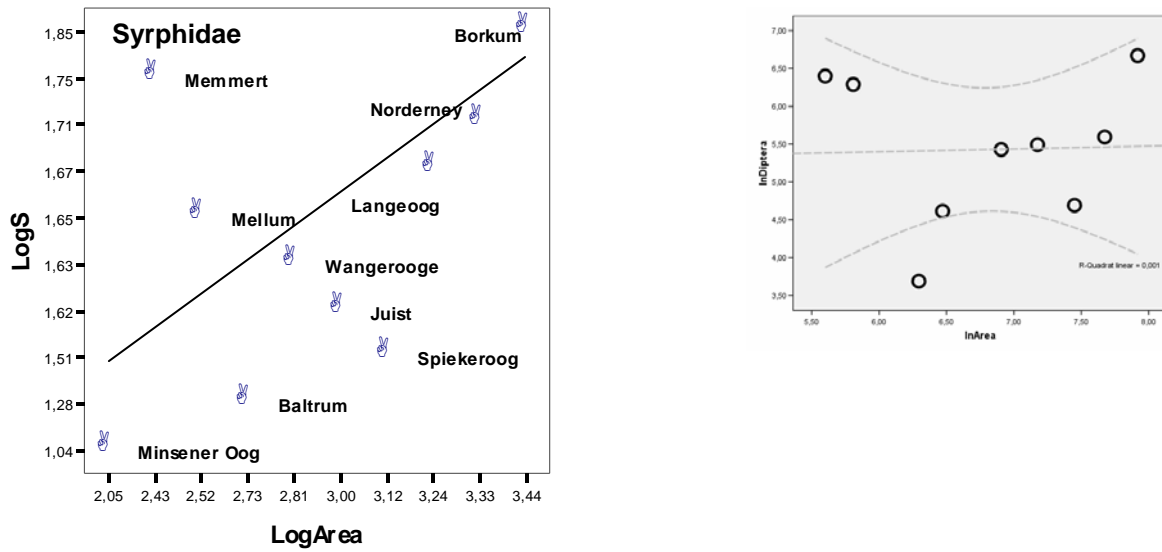


Figure 7: Species-area-relation for Hoverflies (left, including the regression line,  $R = 0.64$ ,  $p < 0.05$ , slope = 0,35) and all Diptera (right, not significant) found on the East-Frisian Islands (log-transformation of the variables, data according to Bröring 2008 and Niedringhaus et al. 2008).

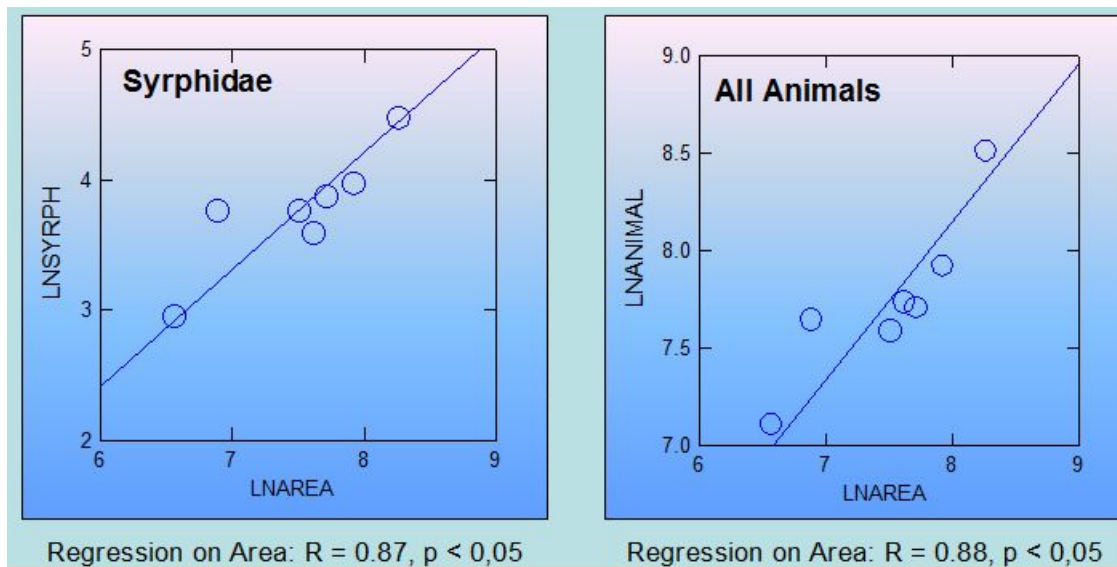


Figure 8: Results of regression analysis between number of species and area size of islands (log-transformation of the variables, data according to Bröring 2008 and Niedringhaus et al. 2008).

There is a reasonable and significant correlation between the number of hoverfly-species and areas size, the correlation coefficient is similar to the overall species area relation of all animal species (fig. 8). Within the analysis data for the young island Memmert and Mellum are excluded due to the serious differences in the sampling intensity.

The number of species and habitat between heterogeneity is not correlated, while habitat within heterogeneity (i.e. number of plant species on the islands) is highly correlated with the number of hoverfly-species (fig. 9).

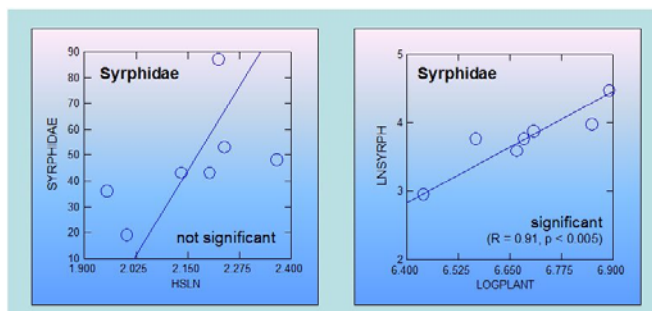


Figure 9: Results of regression analysis between species numbers and habitat between heterogeneity (left) and habitat within heterogeneity (right) (log-transformation of the variables except habitat heterogeneity, data according to Bröring 2008 and Niedringhaus et al. 2008).

Furthermore, there is a significant correlation of species number to the number of human inhabitants on the islands, at least for the number of hoverfly species (fig. 10). Human activities often lead to diversification of habitats, as many Diptera-species occur in or near villages and urban areas. The correlation is slightly significant for the Syrphidae, presumably a stronger relation will be found when all groups of diptera are included.

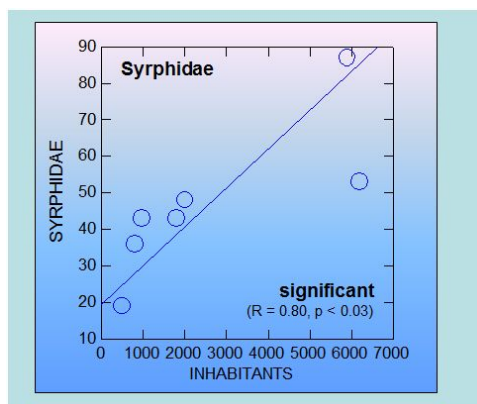


Figure 10: Results of regression analysis between number of species and area number of inhabitants (data according to Niedringhaus et al. 2008).

## 6 Biogeography: Island Colonization

Increase of species numbers in time can be analyzed with data from the young island Memmert and Mellum and the old East Frisian Island Borkum for the family of hoverflies.

On Memmert, 40 years after this small island emerged the middle tide flood line 48 species of hoverflies colonized the island, which is 12 % of all German species! Species turnover is 19 species in 65 years (TR = 32 %). – On Mellum a huge increase of the number of species was observed as well. In 1987 a total of 43 species were found.

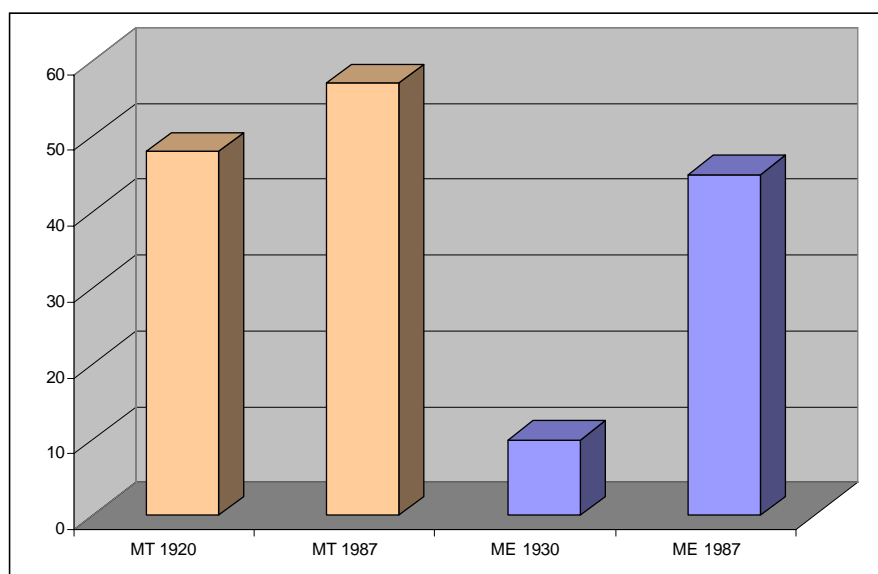


Figure 11: Increase of species numbers on the young islands Memmert and Mellum (Hoverflies, data according to Bröring 2008).

The increase of hoverfly-species on Borkum (fig. 12) is just due to sampling activities: up to 1900: 35 species known for Borkum, up to 1935: 64 species, up to 1985: 73 species known, within the first intercensus interval 65 species have been confirmed, whereas 22 species were found for the first time. By this, to date, 16 % of all species known for the area of Germany are present on Borkum at least temporarily.

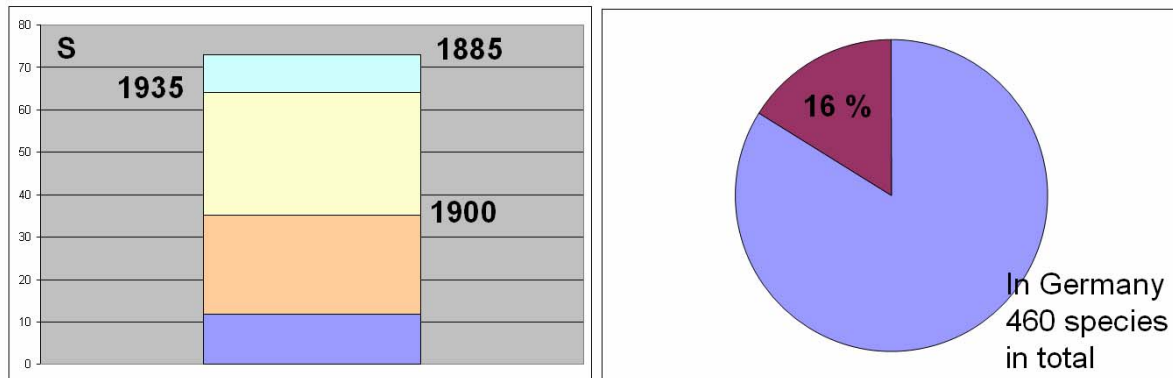


Figure 12: Increase of species numbers of hoverflies (Syrphidae) known for the East Frisian island of Borkum since 1885 (data from Bröring 2008).

## Colonization of the Islands

Our results have shown:

- Many species of diptera have strong colonization ability (high migration rates, and high dispersion ability, resp.).
- The distance to mainland area which is about 5 to 10 km is no barrier for successful transgression for (by far) most of the species. However, successful colonization of the islands is due to the presence of suitable habitats (incl. obligatory hosts).
- Colonization takes place rather rapidly (as shown for the hoverflies on young islands).
- Diversification and disturbance often lead to an increase of species numbers in Diptera.

## 7 Outlook: Further and Additional Research

There is a reasonable and serious lack of knowledge as to the presence and abundance of Diptera on the East Frisian islands and the biology of the various groups, so that further investigations are necessary. The most important aspects are:

- The number of island species is still unknown, for most of the occurring families only rough estimations are available.

- There is a reasonable lack of knowledge as to the general biology of many species of Diptera. There is still a reasonable number of undescribed species also in central Europe.
- Information on the colonization of the various habitats on the islands is still lacking: Which habitats are colonized to what extent, and what about the species composition within habitats?
- What about interactions within the various animal groups like parasitism, predation, disease, and competition?

## 8 Acknowledgements

Sincere thanks to W. Adaschkewitz (Jena), M. v. Tschirnhaus (Bielefeld), F. Püchel-Wieling (Bielefeld) for various help. – Special thanks are due to W. Barke-meyer (Flensburg) for systematic and taxonomic revision of the data set. - Again, many thanks to F. Sick (Kiel) for the scientific management of a former version of the island Diptera species list from 1991. – Many thanks as well to M. Stöckmann (Oldenburg) and V. Haeseler (Oldenburg) for the beautiful pictures I used in my presentation. – And, of course, thanks to R. Niedringhaus (Oldenburg) for good cooperation and enlightening discussions.

## 9 References

Former compilation of East Frisian Flora and Fauna

Bröring, U., Dahmen, R., Haeseler, V., Lemm, R. Von, Niedringhaus, R. & Schultz, W. 1993. Dokumentation der Daten zur Flora und Fauna terrestrischer Systeme im niedersächsischen Wattenmeer. Band 1 und 2. Berichte aus der Ökosystemforschung Wattenmeer 4/1992. 119 + 207 pp.

The „Blue Book“

Niedringhaus, R. Janiesch, P. & Haeseler, V. (Hrsg.). 2008. Die Flora und Fauna der Ostfriesischen Inseln. Schr.-R. Nationalpark Nieders. Wattenmeer 11: 470pp.

Niedringhaus, R. Janiesch, P. & Haeseler, V. (Hrsg.). 2008. Short Version. <http://www.natosti.uni-oldenburg.de/>

Diptera Nematocera

Niedringhaus, R. 2008. Zur Mückenfauna der Ost-Friesischen Inseln (Diptera: Nematocera). In: Niedringhaus, R. Janiesch, P. & Haeseler, V. (Hrsg.), Die Flora und Fauna der Ostfriesischen Inseln. Schr.-R. Nationalpark Nieders. Wattenmeer 11: 341-348.

## Diptera Brachycera Orthorrhapha

Bröring, U. & Niedringhaus, R. 2008. Niedere Fliegen der Ostfriesischen Inseln (Diptera: Brachycera: Orthorrhapha: (Stratiomyidae, Rhagionidae, Therevidae, Scenopinidae, Asilidae, Bombyliidae, Tabanidae). In: Niedringhaus et al. (Hrsg.), op. cit.: 349-353.

Meyer, H. & Schleppegrell, M. 2008. Langbein-, Tanz- und Rennraubfliegen der ostfriesischen Düneninseln (Diptera: Brachycera: Orthorrhapha: Empidoidea: Dolichopodidae, Microphoridae, Empididae, Hybotidae). In: Niedringhaus et al. (Hrsg.), op. cit.: 355-364.

## Diptera Brachycera Cyclorrhapha

Bröring, U. 2008. Die Schwebfliegen und verwandte Gruppen der Ostfriesischen Inseln (Diptera: Brachycera: Cyclorrhapha: Aschiza). Schweb-, Augen-, Lanzen-, Tummel- und Buckelfliegen (Syrphidae, Pipunculidae, Lonchopteridae, Platyppezidae, Phoridae). In: Niedringhaus et al. (Hrsg.), op. cit.: 365-371.

Tschirnhaus, M. v. 2008. Die acalyptraten Fliegen der Ostfriesischen Inseln (Diptera: Schizophora, Acalyptratae). Kritisches Artenverzeichnis anhand von Literaturdaten, Neufunden und unter Mitarbeit von Fachkollegen. In: Niedringhaus et al. (Hrsg.), op. cit.: 373-390.

Bröring, U. 2008. Über das Vorkommen von calyptraten Fliegen auf den Ostfriesischen Inseln (Diptera: Brachycera: Cyclorrhapha: Schizophora: Calyptratae). In: Niedringhaus et al. (Hrsg.), op. cit.: 391-399.

## Additional Information on Island Flora and Fauna, Study sites and Landscape

Niedringhaus, R., Haeseler, V & Janiesch, P. 2008a. Einführung in das Projekt. In: Niedringhaus et al. (Hrsg.), op. cit.: 9-34.

Niedringhaus, R., Haeseler, V & Janiesch, P. 2008b. Die Ostfriesischen Inseln als Lebensraum einer einzigartigen Flora und Fauna. In: Niedringhaus et al. (Hrsg.), op. cit.: 453-468.

## References (Diptera Systematics)

Schumann, H., Bährmann, R. & Stark, A. 1999. Entomofauna Germanica. Checkliste der Dipteren Deutschlands. *Studia Dipterologica*. Suppl. 2: 354pp.

Schumann, H. 2002. Erster Nachtrag zur Checkliste der Dipteren Deutschlands. *Studia Dipterologica* 9: 437-445.

Schumann, H. 2004. Zweiter Nachtrag zur Checkliste der Dipteren Deutschlands. *Studia Dipterologica* 11: 619-613.

Soos, A. & Papp, L. 1984. *Catalogue of the Palaearctic Diptera*. Vol. I-X. Budapest.

Fauna Europaea 2004ff. [<http://www.faunaeur.org/>] [last check April 2008]

## Further Readings

- Bröring, U. 1992. Dokumentation floristischer und faunistischer Daten der terrestrischen Systeme im Niedersächsischen Wattenmeer. Berichte aus der Ökosystemforschung Wattenmeer 1/1992. 2. Symp. Ökosystemforschung Wattenmeer in Büsum: 88-90.
- Haeseler, V. & Meyer, K.-O. (red.) 1988. Zoologische Beiträge zur Besiedlung der jungen Düneninseln Memmert und Mellum. Drosera ` 88 Supplement, Oldenburg: 369pp.
- Haeseler, V. 1988. Entstehung und heutiger Zustand der jungen Düneninseln Memmert und Mellum sowie Forschungsprogramm zur Besiedlung durch Insekten und andere Gliederfüßer. Drosera ` 88: 5-46.
- Niemeyer, G. 1972. Ostfriesische Inseln. Berlin, Stuttgart.
- Schneider, O. 1898. Die Tierwelt der Nordseeinsel Borkum unter Berücksichtigung der von den anderen Inseln bekannten Arten. Abh. Naturwiss. Ver. Bremen 16: 174pp.
- Streif, H. 1990. Das ostfriesische Küstengebiet. Nordsee, Inseln, Watten und Marschen. Sammlung geologischer Führer 57. Berlin, Stuttgart.
- Streif, H. 1989. Barrier islands, tidal flats, and coastal marshes resulting from a relative rise of sea level in East Frisia and the German North Sea Coast. Proc. KNGMG Symp. Coastal Lowlands, Geology and Geotechnology (1987): 213-223.

## Further Readings (Island Biogeography)

- Boomsma, J., Mabeles, A., Verbeek, M., Los, E. 1987. Insular biogeography and distribution ecology of ants on the Frisian islands. J. Biogeogr. 14: 21-37.
- Bröring, U. 1991. Die Heteropteren der Ostfriesischen Inseln. Ein Beitrag zur Inselbiogeographie. Oldenburg: 96pp.
- Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113: 791-833.
- Hubbel, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology. Princeton: 375p.
- MacArthur, R. & Wilson, E.O. 1967. The theory of island biogeography. New York.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity, Part I. and II. Ecology 43 (2,3. 185-215, 410-432.

For some background information check:

- Bröring, U. 2007. Basics of island biogeography. The equilibrium theory of island biogeography. Script; or: Die Gleichgewichtstheorie der Inselbiogeographie. Scriptum. <http://www.tu-cottbus.de/fakultaet4/de/oekologie/lehrstuhl/mitarbeiterinnen/pd-dr-rer-nat-habil-udo-broering/vortraegelehrveranstaltungen-presentationslectures.html> .