# Proceedings *of the* Netherlands Entomological Society Meeting

# 2005 *volume* 16

# Aggregation of water beetles: mechanisms of dispersal

**W.C.E.P. Verberk & H. Esselink**
Bargerveen Foundation & Department of Animal Ecology and Ecophysiology, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands; E-mail: W.Verberk@science.ru.nl

Aquatic beetles occupy a complete range of wetland habitats, but individual species of water beetles use their surroundings on different spatial and temporal scales. What a species needs and what the environment supplies is scale specific and species specific. This type of knowledge provides important information on the possibilities species have to deal with environmental challenges, such as coping with temporary water bodies. This in turn is important in the practice of restoration management because, with this type of information, effects of measures on the species present can be predicted.
However, for individual species, this type of knowledge is largely lacking. Therefore invertebrates were sampled repeatedly in two water types. Different parts within a water body were sampled separately. In autumn a strong aggregation of water beetles in floating rafts was found in both water bodies. Floating rafts are the result of bottom material and vegetation gaining buoyancy due to methane production. These rafts offer a temporary supply of nutrients in the form of detritus and algae. Data on flight capability, data on species occurrences in other parts in the water body and data from previous seasons were analysed to determine the mechanism of dispersal (from other parts within the water body or from other nearby water bodies). Rafts were dominated by good dispersers, which were locally abundant, with mainly crawling, herbivorous and detritivorous species.
This study highlights one particular strategy on how species abilities and landscape characteristics can match on a specific scale in space and time. This strategy can also be important in an intact raised bog landscape.

*Keywords:* scale, landscape, life history tactic, aquatic invertebrates, restoration management

Water beetles form an important part of aquatic invertebrate assemblages, especially in stagnant, shallow water bodies with a well-developed vegetation (Foster *et al.* 1992, Fairchild *et al.* 2000). This group is diverse, comprising many different species (little under 300 species in The Netherlands) from different families and subfamilies. They are thought to have made the transition to an aquatic life several times during their phylogenetic history (Drost *et al.* 1992). Both adults and larvae are aquatic in most species, although there are some species with an aquatic stage restricted to either adult or larva. There are large differences in size (from 1 to 48 mm) but also with respect to other ecological characteristics such as diet, locomotion (*e.g.* Ribera & Nilsson 1995), and flight (Richoux 1994).

This diversity in ecological attributes enables aquatic beetles as a group to occupy a complete range of wetland habitats, but individual species of water beetles use their surroundings on different spatial and temporal scales (Fairchild *et al.* 2003). On a temporal scale, for example, the duration (semivoltine to multivoltine) and the period of larval development (spring, summer, autumn and winter) differs. On a spatial scale, for example, the type of locomotion (swimming or crawling), and flight capability differs. Therefore, the match between what a species needs and what the environment supplies (Verberk & Esselink 2003) is scale specific and species specific; different water types harbour different species (Verberk *et al.* 2001).

Heterogeneous landscapes can meet the requirements of many different species (additive), but may also further promote species richness in different ways (synergistic; Verberk *et al.* 2002). Water beetles are expected to be facilitated by heterogeneity, because most species are capable of both discerning (well developed eyes) and utilizing heterogeneity (high mobility and mostly long lived). Due to degradation, environmental conditions are deteriorating and as a result some species are no longer able to complete their lifecycle (*i.e.* there is a

*Figure 1.* Floating rafts in autumn. Picture by Wilco Verberk.

bottleneck for that species). Restoration measures aim to restore the environmental conditions and lift existing bottlenecks. However, large scaled restoration measures can result in a decline of heterogeneity (at least in the short term) and may therefore present new bottlenecks for those species depending on heterogeneity (Van Duinen *et al.* 2003, 2004b). In order to minimize negative side effects of restoration measures, more knowledge on the match between species and their environment is needed.

To this end, we investigated the invertebrate assemblage of different microhabitats within a water body in different water types on four occasions, corresponding to the four different seasons (Verberk *et al.*, in prep). In autumn, floating rafts were observed, resulting from bottom material becoming buoyant, held together by roots of shore vegetation (Fig. 1). Increased decomposition, resulting in methane production can cause this phenomenon (Smolders *et al.* 2002). On these rafts, high numbers of aquatic beetles were found (Fig. 2). Methane is produced anaerobically, and when the upper part becomes floating atmospheric oxygen further increases the decomposition, aerobically. The high decomposition rates produce much detritus and increase the release of nutrients, stimulating primary, algal production. These floating rafts can therefore offer a temporary supply of nutrients in the form of detritus and algae.

To gain a better understanding of how species utilize this temporary supply of food, this paper addresses the following questions: (1) What are the differences in species composition between the rafts and other microhabitats in autumn? (2) What are differences in ecology of species found in rafts and other microhabitats in autumn? (3) Where do the species found in the rafts come from?

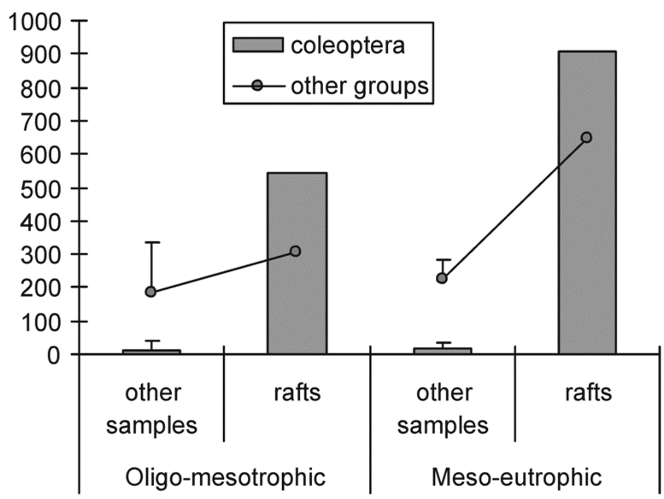


*Figure 2.* Abundance of waterbeetles and other taxonomic groups in autumn. Results are shown separately for the two watertypes and for rafts and other samples.

# MATERIAL AND METHODS

## Study area and sample locations

The water bodies sampled are located in the bog remnant Korenburgerveen (described in detail in Verberk *et al.* 2001, 2004). Both water bodies are bomb pits and at their location cover sands reach the surface. As a result these water bodies are buffered. The meso-eutrophic water body has the highest alkalinity and the water is almost completely covered by floating *Potamogeton natans* with *Typha latifolia* and *Carex rostrata* on the shore. The oligo-mesotrophic water has a low alkalinity. *Potamogeton natans* occurs locally in the water body and *Eriophorum vaginatum* is abundant on the shores. The water bodies are adjacent (<10 m apart) with *Myrica gale* and *Molinia caerulea* dominating the surrounding vegetation.

## Invertebrate collection

Invertebrates were collected during four sampling periods, hereafter referred to as winter data (5, 7 and 12 February 2003), spring (1-3 April 2003), summer (25-27 June 2003) and autumn (12, 15 and 19 September 2003). In each water body different vegetation structures were sampled separately. Based on the structure, these samples could be classified into one or two of seven different categories of microhabitat: Shore, *Sphagnum*, thin emergent vegetation (*Eriophorum*, *Carex*), robust emergent vegetation (*Typha*), floating vegetation (*Potamogeton*), Bottom, Open water. In this paper, floating rafts are an extra separate category, but are elsewhere (Verberk *et al.*, in prep) classified as a mixture of shore and fine emergent vegetation.

Samples were taken in a semi-quantitive way, aimed at obtaining a complete list of the occurring invertebrates. Sample material was collected using a kitchen sieve (mesh size of 1.0 mm) and dip net (mesh size of 0.5 mm) and samples were sorted in the field using white trays. This enabled the collecting of additional material if prior catches had yielded only few animals. Sampling effort was kept equal for the different microhabitats at approximately 4 man hours sorting time, with the exception of open water, for which sampling and sorting took less time (approximately 0.5 h).

## Data analysis

To functionally interpret differences in species composition and abundance, a number of ecological attributes were looked up in literature. Feeding guild was subdivided in three classes (herbivorous, detritivorous, carnivorous). Type of locomotion (aquatic mobility) was subdivided in two classes (crawler, swimmer). For each attribute, a species scored 1 for the appropriate class. If more than one class applied to a species (*e.g.* omnivores), their score was divided over all appropriate classes up to a total of 1. Data was derived from (Richoux 1994, Nilsson & Holmen 1995).

Species dispersal (aerial mobility) was classified as non-dispersive (0), dispersive (1) or highly dispersive (2) using a range of literature (references in Lundkvist *et al.* 2002, Drost *et al.* 1992).

The local status of species (their abundance in the neighbourhood) was based on extensive research on invertebrates in the nature reserve Korenburgerveen (Verberk & Esselink 2004). Based on the frequency and abundance of species found in this study, species were classified arbitrarily into three classes of increasing abundance: scarce, occasional, abundant. The fourth class was comprised of species not found during this study.

To derive the origin of species (within the water body, or from nearby water bodies), species were assigned to different groups of mobility. Species assignment was based on their abundance in the rafts of both water bodies, relative to their abundance in other parts of the water body and relative to their abundance in previous seasons.

Species assigned to the locomotion group (aquatic movement) are presumed to have moved from other parts of the water body to the rafts. These species either had low abundances in the rafts, or numbers found in previous seasons could account for their higher abundances. Species assigned to the dispersal group (aerial movement) are presumed to have originated from nearby water bodies through aerial dispersal. These species had high abundances in rafts compared to other parts of the water body and numbers found in previous seasons could not account for that. Dispersers could be selective (preference for rafts in one of the two water bodies), or aselective (preference for rafts equal in both water bodies). Species with insufficient data were assigned as unknown.

## RESULTS

The species composition differed between the rafts and other samples taken in autumn (Table 1), with more Hydraenidae and Hydrophilidae (*e.g. Hydreana testacea, Cymbiodyta marginella*) and less Dytiscidae (*e.g. Suphrodytes dorsalis*) and Noteridae in the rafts. This difference was also reflected in the species' ecology, with herbivorous and detritivorous individuals being more abundant in the rafts (Fig. 3a) as well as the number of crawling individuals (Fig. 3b).

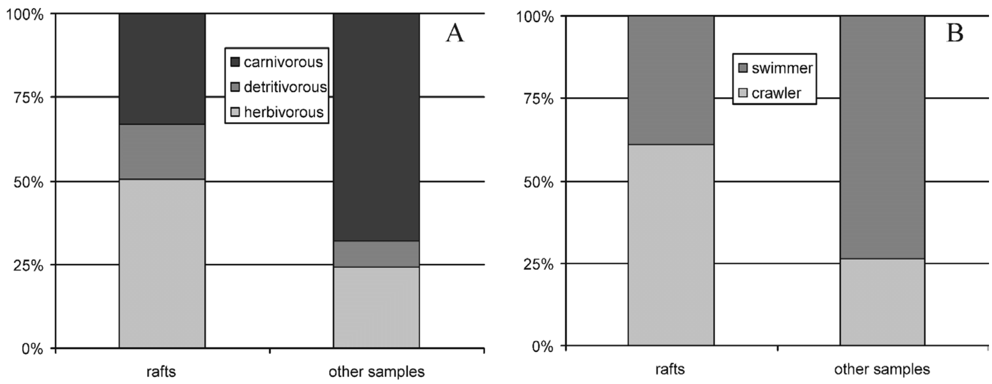


*Figure 3.* Percentage of individuals, subdivided according to food preference (A) and type of locomotion (B).

*Table 1.* Number of individuals found in rafts and other samples in autumn, as well as during previous seasons. For each species, information is given on family, flight capacity, food requirements, rarity, size and their mobility group (see materials and methods). Only species found in the rafts are shown for reasons of clarity.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| a: | abundant | r: | rare | Dry: | Dryopidae | Hyo: | Hydrochidae |
| o: | occasional | fr: | fairly rare | Dyt: | Dytiscidae | Hyi: | Hydrophilidae |
| s: | scarce | fc: | fairly common | Hal: | Haliplidae | Not: | Noteridae |
| x: | not previously found | c: | common | Hel: | Helophoridae | Sci: | Scirtidae |
| vr: | very rare | vc: | very common | Hya: | Hydraenidae | | |

| | Family | Mesotrophic water body | | | | | Eutrophic water body | | | | | Locomotion | | Flight capacity | Food | | | Mobility group | | | | Rarity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | raft samples | other samples | summer | spring | winter | raft samples | other samples | summer | spring | winter | swimmer | crawler | | plants - algae | detritus | animals | Unknown | Locomotion | Flight selective | Flight aselective | Local status |
| Anacaena lutescens | Hyi | 1 | 5 | 4 | 1 | 0 | 39 | 2 | 1 | 1 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 1 | 0 | a |
| Copelatus haemorrhoidalis | Dyt | 5 | 0 | 0 | 1 | 0 | 6 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Copelatus haemorrhoidalis lr | Dyt | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Cymbiodyta marginella | Hyi | 141 | 9 | 0 | 0 | 0 | 171 | 2 | 0 | 5 | 0 | 0 | 1 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 0 | 1 | o |
| Enochrus affinis | Hyi | 33 | 1 | 0 | 2 | 0 | 14 | 1 | 6 | 1 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 0 | 1 | a |
| Enochrus coarctatus | Hyi | 32 | 21 | 6 | 1 | 0 | 70 | 1 | 9 | 3 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 0 | 1 | o |
| Enochrus sp lr | Hyi | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 27 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | a |
| Graptodytes granularis | Dyt | 2 | 1 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | s |
| Helochares punctatus | Dyt | 28 | 17 | 0 | 4 | 1 | 8 | 1 | 10 | 0 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 1 | 0 | o |
| Helochares sp lr | Dyt | 3 | 2 | 13 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | o |
| Hydraena palustris | Dyt | 1 | 0 | 0 | 0 | 0 | 24 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 1 | 0 | o |
| Hydraena testacea | Dyt | 38 | 14 | 0 | 0 | 0 | 30 | 0 | 3 | 0 | 0 | 0 | 1 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 0 | 1 | s |
| Hydrochus carinatus | Dyt | 10 | 9 | 1 | 0 | 0 | 35 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | o |
| Hydroporus angustatus | Dyt | 43 | 32 | 1 | 11 | 2 | 54 | 9 | 4 | 20 | 3 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Hydroporus scalesianus | Dyt | 10 | 1 | 1 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Hydroporus tristis | Dyt | 4 | 2 | 0 | 1 | 1 | 24 | 3 | 1 | 2 | 7 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | a |
| Hydroporus umbrosus | Dyt | 30 | 28 | 2 | 20 | 0 | 20 | 3 | 7 | 8 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | a |
| Hygrotus decoratus | Dyt | 13 | 25 | 0 | 2 | 0 | 141 | 20 | 6 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | a |
| Hygrotus decoratus lr | Dyt | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | a |
| Ilybius ater | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Ilybius ater lr | Dyt | 5 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | o |
| Limnebius aluta | Dyt | 82 | 32 | 0 | 0 | 0 | 159 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 0 | 1 | s |
| Ochthebius minimus | Dyt | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0.8 | 0.3 | 0 | 0 | 0 | 1 | 0 | x |
| Agabus bipustulatus | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Agabus bipustulatus lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Anacaena limbata | Hyi | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 1 | 0 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 0 | 1 | 0 | 0 | o |
| Coelostoma orbiculare | Hyi | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0.5 | 0.5 | 0 | 0 | 1 | 0 | 0 | x |
| Cyphon sp lr | Sci | 1 | 4 | 15 | 0 | 1 | 9 | 0 | 14 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | a |
| Haliplus confinis | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | x |
| Haliplus confinis lr | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | x |
| Helophorus sp | Dyt | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | s |
| Hydaticus seminiger | Dyt | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | o |
| Hydroporus erythrocephalus | Dyt | 6 | 1 | 1 | 1 | 0 | 6 | 4 | 5 | 3 | 7 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Hygrotus inaequalis | Dyt | 10 | 1 | 2 | 2 | 0 | 0 | 3 | 0 | 1 | 4 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Hygrotus inaequalis lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Nartus grapii | Dyt | 0 | 1 | 0 | 2 | 0 | 4 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | s |
| Nartus grapii lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | s |
| Noterus clavicornis | Dyt | 9 | 2 | 3 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | s |
| Noterus crassicornis | Dyt | 1 | 3 | 0 | 1 | 0 | 24 | 3 | 17 | 31 | 4 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | a |
| Suphrodytes dorsalis | Dyt | 0 | 3 | 0 | 2 | 0 | 5 | 7 | 2 | 0 | 11 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | o |
| Suphrodytes dorsalis lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | o |
| Colymbetes paykulli | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | s |
| Haliplus cf ruficollis | Dyt | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | o |
| Haliplus gr ruficollis lr | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | o |
| Hydrobius fuscipes | Dyt | 11 | 0 | 0 | 2 | 0 | 4 | 0 | 2 | 0 | 0 | 0.5 | 0.5 | 2 | 0.8 | 0.3 | 0 | 1 | 0 | 0 | 0 | a |
| Hydrobius fuscipes lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | a |
| Hydrochus brevis | Dyt | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | s |
| Hydroglyphus pusillus | Dyt | 5 | 0 | 0 | 0 | 0 | 4 | 1 | 3 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | s |
| Hydroporus palustris | Dyt | 0 | 1 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | o |
| Ilybius aenescens | Dyt | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | a |
| Ilybius aenescens lr | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | a |
| Ilybius guttiger | Dyt | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | a |
| Ilybius guttiger lr | Dyt | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | a |
| Laccobius bipunctatus | Dyt | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0.5 | 0.5 | 1 | 0.8 | 0.3 | 0 | 1 | 0 | 0 | 0 | s |
| Laccophilus minutus | Dyt | 1 | 3 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | s |
| Peltodytes caesus | Dyt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | o |

Both the rafts and the other samples were numerically dominated by species, which are presumed to have -by means of aerial movement- immigrated to the water body from the surrounding water bodies (dispersal group; Fig. 4). This presumption was based data collected in this research (abundances of species in the rafts, other microhabitats as well as abundances during previous sampling periods) and was in agreement with literature data on species dispersal (Fig. 5). Species not capable of flight (*Noterus crassicornis and Hydroporus obscurus*) were either presumed to have moved -by means of aquatic movement- within a water body (locomotion group) or not found in the rafts. Within the dispersal group, species known from literature to be very mobile, were all aselective dispersers, having an equal preference for rafts in both water bodies. Common and uncom-

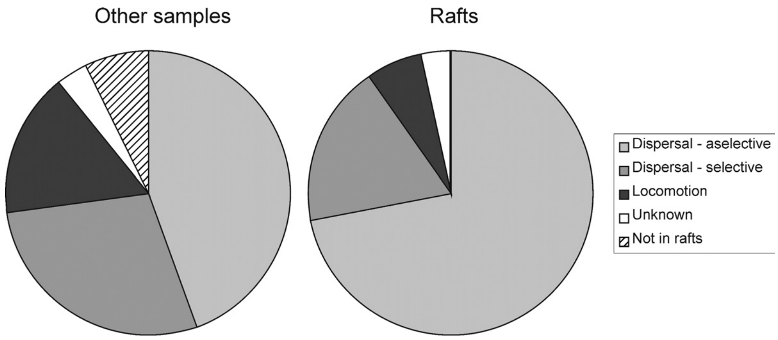


*Figure 4.* Percentage of individuals, subdivided according to mobility group, shown separately for rafts and other samples in autumn.

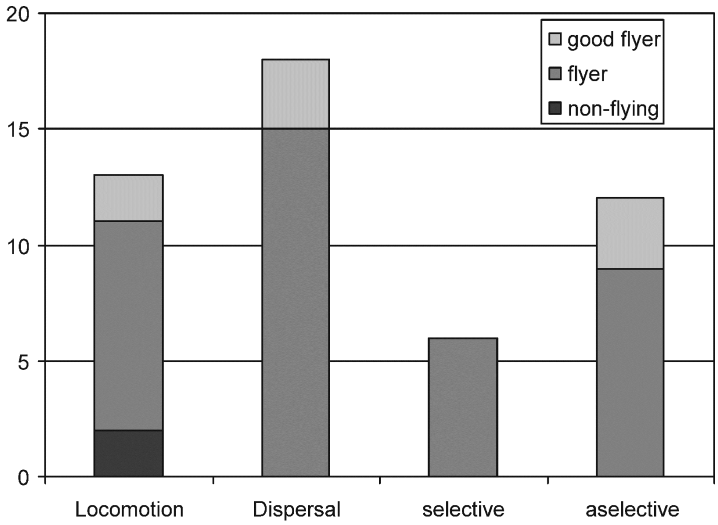


*Figure 5.* Number of species with good, normal or no flight capability according to literature. Results are shown separately for different mobility groups, with dispersal subdivided in selective and aselective dispersal.

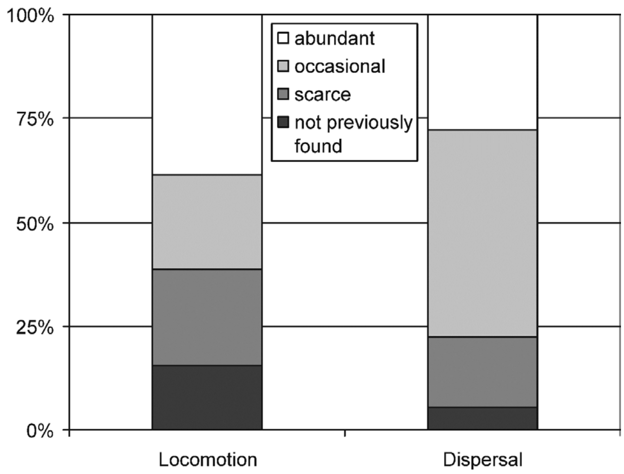


*Figure 6.* Local status of species (expressed as species percentage) based on surveys in the area (Verberk *et al.* 2004).

mon species dominated the dispersal group (Fig. 6). Species, which were locally rare or not previously found, made up a higher percentage in the locomotion group (Fig. 6).

Size of species differed, with species in the dispersal group (both selective and a selective) being significantly smaller compared to those species classified either in the locomotion group or not found in rafts (student t-test, two-tailed distribution, unequal variance assumed: $P=0.0039$).

## DISCUSSION

Floating rafts offer a temporary supply of nutrients in the form of detritus and algae. As a result, the beetle assemblage of floating rafts is characterized by good dispersers, which are locally abundant, with mainly crawling, herbivorous and detritivorous species. Some species were carnivores but they probably moved there from other parts of the water body (*Hygrotus inaequalis*) or deposited eggs there (*e.g. Ilybius ater*). For carnivores, deposition of eggs can be advantageous, as the secondary production (biomass of detritivores and herbivores) ensures a good food supply for their carnivorous larvae. Moller Pillot (2003) also found that temporal changes in food supply can have a profound influence on the invertebrate assemblage.

Species classified in different mobility groups differed in size, with dispersers being smaller. Smaller, crawling beetles could be more mobile on the (semi-terrestrial) rafts, but size is also linked with *e.g.* development time and food requirements. Smaller beetles are expected to require less food, or to be satiated more quickly. This could be an adaptation to the temporary nature of these food sources in floating rafts. Most species probably do not reproduce in these rafts as most species reproduce in the summer (Richoux 1994). More likely, these species use the rafts as an energy source for *e.g.* hibernation and egg development. In a study on dispersing diving beetles (Dytiscidae), Lundkvist *et al.* (2002) observed two peaks in dispersal with females being more coming in the first period (April-July) than during the second period (August-October), suggesting directed migration in spring-summer for reproduction and opportunistic dispersal in autumn.

In short, the rafts are an abundant source of food, which are detected and consequently exploited by dispersive, small coleoptera. Such a strategy requires good visual or olfactory powers to locate these temporary food sources. As such, it is a strategy to cope with heterogeneity over long distances and short duration. This strategy can also be important in an intact raised bog landscape. In Estonia's raised bogs there are also spots where decomposition overrules primary production (Karofeld 2004). These are usually hollows which are inundated for long times, leading to anaerobic conditions. During summer and autumn, these spots become dryer and influenced by atmospheric oxygen decomposition rates increase.

This study provides data on species migration and species dispersal capability. This data is derived from seasonal and spatial changes in species abundance. Despite direct information from studies on trapping flying beetles this indirect information is also valuable as aerial traps are invariable biased towards some species and do not always reflect the species composition found in waters nearby (Lundkvist *et al.* 2002). In this study, species belonging to the dispersal group agreed well with the local status of species and with literature information on flight. This provides important information on the possibilities species have to deal with environmental challenges, such as coping with temporary water bodies (Van Duinen *et al.* 2004a). This in turn is important in the practice of restoration management because, with this type of information, the effects that restoration measures have on the species present, can be predicted (see also Van Kleef *et al.*, in prep).

**Acknowledgements** We thank Peter Spierenburg, Martijn Dijkman, Paul van Hoek, Lisa Wiesmann, Judith Bosman and Wouter Nijssen for providing logistic support in the field and identification of water beetles. We thank Marij Orbons for her assistance in the laboratory. In addition, we thank Vereniging Natuurmonumenten and the caretaker of Korenburgerveen, Han Duyverman, for information about the area and permission to enter the reserve and collect samples. This research project was financed by the Dutch Ministry of Agriculture, Nature Management and Fisheries (project number 3911773).

## REFERENCES

Drost, M.B.P., H.P.J.J. Cuppen, E.J. van Nieukerken & M. Schreijer (red.) 1992. *De waterkevers van Nederland*. Uitgeverij KNNV, Utrecht.

Fairchild, G.W., A.M. Faulds & J.F. Matta, 2000. Beetle assemblages in ponds: effects of habitat and site age. *Freshwater Biology* 44: 523-534.

Fairchild G.W., J. Cruz, & A.M. Faulds, 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent pods. *Journal of the North American Benthological Society* 22: 224-240.

Foster, G.N., B.H. Nelson, D.T. Bilton, D.A. Lott, R. Merrit, R.S. Weyl & M.D. Eyre, 1992. A classification and evaluation of Irish water beetle assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2: 185-208.

Karofeld, E. 2004. Mud-bottom hollows: exceptional features in carbon-accumulating bogs? *The Holocene* 14: 119-124.

Lundkvist, E., J. Landin & F. Karlsson, 2002. Dispersing diving beetles (Dytiscidae) in agricultural and urban landscapes in south-eastern Sweden. *Annales Zoologici Fennici* 39: 109-123.

Moller Pillot, H.K.M., 2003. Hoe waterdieren zich handhaven in een dynamische wereld. 10 jaar onderzoek in de Roodloop, een bovenloopje van de Reusel in Noord-Brabant. Stichting Noordbrabants Landschap, Haaren.

Nilsson, A.N. & M. Holmen, 1995. The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. II. Dytiscidae. *Fauna Entomologica Scandinavica*, vol. 32.

Richoux, P. 1994. Theoretical habitat templets, species traits, and species richness: aquatic Coleoptera in the Upper Rhône River and its floodplain. *Freshwater Biology* 31: 377-395.

Ribera, I. & A.N. Nilsson, 1995. Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, and Dytiscidae). *Canadian Journal of Zoology* 73: 2343-2360.

Smolders, A.J.P., H.B.M. Tomassen, L.P.M. Lamers, B.P. Lomans & J.G.M. Roelofs, 2002. Peat bog restoration by floating raft formation: the effects of groundwater and peat quality. *Journal of Applied Ecology* 39: 391-401.

Van Duinen, G.A., A.M.T. Brock, J.T Kuper, R.S.E.W. Leuven, T.M.J Peeters, J.G.M. Roelofs, G. van der Velde, W.C.E.P. Verberk & H. Esselink, 2003. Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetland Ecology and Management* 11: 447-459.

Van Duinen, G.A., A. Drees & H. Esselink, 2004a. Importance of permanent and temporary water bodies for aquatic beetles in the raised bog remnant Wierdense Veld. *Proceedings of the Netherlands Entomological SocietyMeeting* 15: 15-20.

Van Duinen, G.A., H.H. van Kleef, M. Nijssen, C.A.M. van Turnhout, W.C.E.P. Verberk, J. Holtland & H. Esselink, 2004b. Schaal en intensiteit van herstelmaatregelen: Hoe reageert de fauna? In: G.A. van Duinen *et al.* (eds.), Duurzaam natuurherstel voor behoud van biodiversiteit – 15 jaar herstelmaatregelen in het kader van het overlevingsplan bos en natuur, pp. 189-240. Rapport EC-LNV nr. 2004/305, Ede.

Van Kleef, H.H., W.C.E.P. Verberk, R.S.E.W. Leuven, G.A. van Duinen, G. Van der Velde & H. Esselink, in prep. Biological traits explain the effects of restoration management on macroinvertebrates in shallow softwater lakes.

Verberk, W.C.E.P., G.A. van Duinen, T.M.J. Peeters & H. Esselink, 2001. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. *Proceedings Experimental and Applied Entomology* 12: 121-128.

Verberk, W.C.E.P., A.M.T. Brock, G.A. van Duinen, M. van Es, J.T. Kuper, T.M.J.

Peeters, M.J.A. Smits, L. Timan & H. Esselink, 2002. Seasonal and spatial patterns in macroinvertebrate assemblages in a heterogeneous landscape. *Proceedings Experimental and Applied Entomology* 13: 35-43.

Verberk, W.C.E.P. & H. Esselink, 2003. Restoring fauna diversity requires an integration of animal ecology and landscape ecology. *Landschap* 20: 3-7. (in Dutch, with English summary)

Verberk, W.C.E.P., H.H. van Kleef, M. Dijkman, P. van Hoek, P. Spierenburg & H. Esselink, in prep. Seasonal changes in invertebrate assemblages: effects of microhabitat and water type.

Verberk, W.C.E.P. & H. Esselink, 2004. *OBN-project: 'Invloed van aantasting en maatregelen op de faunadiversiteit in een complex landschap. Case studie: Korenburgerveen* (eindrapportage 1e fase). Rapport EC-LNV nr 2004/234-O Ede, 86 pp.

Proceedings of the 16th annual meeting of entomologists in The Netherlands, jointly organized by the Section Experimental and Applied Entomology (SETE) of the Netherlands Entomological Society (NEV) and the CEES-Section Evolutionary Genetics, Groningen University

*Proceedings of the Netherlands Entomological Society Meeting*
[abbreviated as: *Proc. Neth. Entomol. Soc. Meet.*]
Volume 16 (2005)
Editor: Jan Bruin (Section Population Biology, University of Amsterdam)

ISBN 90 71912 26 4


Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands
[http://www.nev.nl]

Copies of the Proceedings (and back volumes) may be ordered from the NEV

Main sponsor of the meeting was:

KOPPERT
BIOLOGICAL SYSTEMS