van zee tot land

PATCHWORK

PATCH USE, HABITAT EXPLOITATION AND CARRYING CAPACITY FOR WATER BIRDS IN DUTCH FRESHWATER WETLANDS

Mennobart R. van Eerden

PATCHWORK
PATCH USE, HABITAT EXPLOITATION AND CARRYING CAPACITY
FOR WATER BIRDS IN DUTCH FRESHWATER WETLANDS

UITNODIGING

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Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands

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Van Zee tot Land 65

Front cover: Purple Swamp-hens *Porphyrio porphyrio*, a characteristic
but threatened bird of Mediterranean freshwater marshes.
Detail of mosaic floor *c.* 30-50 A.D. Dougga, Tunisia.

CONTENTS

Voorwoord

Mijn eerste contacten met vogels kreeg ik via mijn vader; het waren de Koolmezen in het Sterrebos in Groningen die ik op vierjarige leeftijd kreeg voorgeschoteld in 1958, toen ze pinda's namen van mijn hand die ik vol vertrouwen en geduld had uitgestoken op die winterse namiddag. Ik voel de nageltjes nog in mijn vingers. Daarna volgden vele excursies naar eenden, zwanen en Goudplevieren. Mijn moeder bracht me de fascinatie voor planten bij; haar gevoel voor detail en grenzeloos optimisme vormden de basis voor mijn grondhouding. Dat de voorliggende studie in zeven hoofdstukken de relatie plant-dier belicht is daarmee niet zo verwonderlijk meer. Het was Eduard Koopman die me in 1967 in contact bracht met de C.J.N., waar we in teamverband onze biologische interesse verder uit-bouwden. Het bleek een gouden greep en die jeugdbondstijd heeft veel bijgedragen aan het verdere verloop van mijn leven.

Toen ik 30 jaar geleden in oktober 1968 voor het eerst de Lauwerszee zag, tussen Kollumerpomp en de voet van de Wilhelmina trap, zou het niet lang meer duren of het laatste caisson in de afsluitdijk zou worden afgezonken (mei 1969). Daarmee was een einde gekomen aan de estuariene fase die dit gebied heeft gekend sinds de laatste 7000 jaar. Tegelijkertijd was ook in Flevoland de afsluiting van de dijk gerealiseerd en 43 000 ha IJsselmeer-bodem viel droog in 1968. In beide gebieden kwam een ongekend krachtige ontwikkeling op gang wat betreft de kolonisatie door nieuwe plant- en diersoorten. Gefascineerd door deze ontwikkelingen raakte ik betrokken bij het onderzoek. Eerst als vrijwillige vogelteller in de Lauwersmeer, waar ik samen met Jouke Prop enkele duizenden uren heb doorgebracht in de pionierfase van dit gebied (1970-1976). We hadden in die tijd systematische vogeltellingen tussen Vierhuizen en Lauwersoog. Uit die tijd dateren de eerste contacten met de beheerder van het gebied, de R.IJ.P. (Rijksdienst voor de IJsselmeerpolders). Na een doctoraalonderwerp, dat de interactie tussen watervogels en zeekraal betrof, werden de vogeltellingen van de R.U.G. (Rijks Universiteit Groningen) en de R.IJ.P. op elkaar afgestemd in 1976. Datzelfde jaar begon Leo Zwarts bij deze dienst zijn studie naar de relatie tussen vogels en voedsel in de landaanwinningswerken langs de Groninger en later vooral Friese kust. Leo's *Ausdauer* en enthousiasme stimuleerden mij sterk in de wetenschap dat ook langjarig onderzoek in de jonge poldergebieden van "boven regionale" betekenis zou zijn.

Dankzij het feit dat in 1979 een baan vrij kwam bij de biologische afdeling van de R.IJ.P. kon een en ander gerealiseerd worden. Hoewel het Lauwersmeer werk in volle gang was, werd mijn feitelijke opdracht een studie te verrichten naar de draagkracht van het IJsselmeergebied voor watervogels. Dit in verband met de problematiek van de voorgenomen aanleg van de Markerwaard. Ik aarzelde niet lang om ook hier een breed-front onderzoek te starten. Watervogeltellingen werden georganiseerd vanuit de lucht sinds november 1979 en zijn tot op heden continu voortgezet. Met Jan Muller begon ik

verdronken watervogels naar het Smedinghuis in Lelystad te slepen, afkomstig uit de netten van IJsselmeervissers. Met Jan heb ik in tien jaar tijds zo'n 10 000 vogels gesorteerd, gelabeld en gesneden. In afzonderlijke studies werden zowel de duikeenden, zaagbekken, futen, aalscholvers, sterns en meeuwen belicht, meestal met behulp van *hardcore* studenten. Het is hier op zijn plaats de inzet te noemen van Theunis Piersma (Futen), Maarten Platteeuw (zaagbekken en Aalscholvers), Berend Voslamber, Kees Koffijberg, Stef van Rijn (Aalscholvers), Bert Slager, Jan de Vries, Joep de Leeuw (duikeenden) en Kees Schouten (Zwarte Sterns). Met Bram bij de Vaate werd de basis gelegd voor een langdurig meetnet en onderzoek naar de bodemfauna van het IJsselmeer en Markermeer. Met Jan Muller kon ik een haalbaar plan opzetten en uitvoeren voor visbemonstering, "gezien door vogelogen".

Ook het Oostvaardersplassen gebied kreeg steeds meer aandacht. Naast de aalscholverstudie die Menno Zijlstra en ik hier samen zijn begonnen in 1981, stonden Grauwe Gans en Wintertaling centraal in het onderzoek. Bij het Grauwe Gans werk tijdens de vleugelrui speelden Maarten Loonen, Wouter Iedema en Pim Kik een belangrijke rol. Ook in het Lauwersmeergebied liepen een aantal studies door; Jan Beekman, Henk van Huffelen, Maarten Loonen, Bert Slager, Leo Soldaat, Bernard Spaans, Maarten Platteeuw en Dirk Prop, waren belangrijke steunpilaren. Het is opvallend dat verschillende malen dezelfde namen voorkomen: kennelijk werkte het onderzoek verslavend, ook voor de betrokken studenten. De vervangende dienstplicht bood de mogelijkheid langere tijd veldstudies te doen, wat zich ook, gezien de resultaten van deze onderzoekers buiten dit project, heeft geloond. Wat betreft deze studie kan ik stellen dat ik vanaf het begin af aan de overtuiging had breder te moeten kijken dan de feitelijke opdracht. Dat heeft veel tijd gekost maar ook veel opgeleverd; dit voorliggende werk is als een waaier kaarten uit een veel groter spel. Ik heb geprobeerd de verschillende onderdelen die nu beschikbaar zijn zo te rangschikken dat de samenhang duidelijk wordt.

Ook binnen de R.IJ.P. was support aanwezig. Ik waardeer het vertrouwen dat ik al die jaren heb gekregen van Cees Berger, Joost de Jong en Jan van Kampen als de meest direkt betrokkenen gedurende de eerste jaren, later van Matthieu Pinkers, Klaas Feitsma en Bart Fokkens. Hoewel ook bij de desbetreffende hoofdstukken bedankt, past hier nog een speciaal woord van dank voor Jan Muller, Marinus van der Meulen, Bram bij de Vaate, Lambertus Sollie, Wolter Eenkhoorn, Anton Wevers, Bertus van Panhuis en Jaap Bottenberg, allen bij de direkte uitvoering van het veldwerk betrokken. Ik waardeer de opvang en collegialiteit zeer van Menno Zijlstra en Wouter Dubbeldam, de oude rotten in het vak met wie ik zoveel samen heb ondernomen; van hen leerde ik (onder andere) een brug te slaan naar het verleden. Rennie Kuik verzorgde vele jaren de technisch-financiële afwikkeling van al mijn wensen, waarvoor ik hier graag mijn waardering wil uitspreken. Voor de dagelijkse afscherming in de laatste fase van het onderzoek zorgden Albert de Haas en Frederike Kappers. Ik ga ervan uit dat de bij dit onderzoek verkregen inzichten ook in de huidige organisatie, het RIZA, kunnen worden gebruikt ten behoeve van beleid, beheer en ontwikkeling van *wetlands* en natuuronwikkeling in de Rijks-wateren.

30 jaar watervogels, waarvan nu 10 jaar samen met Marjolein. Jouw hulp en systematisch denken waren niet alleen onontbeerlijk voor het onderzoek, je hebt zin gegeven aan ons gezamenlijk streven wat in deze wereld neer te zetten. Ik weet dat je ook na het gereed komen van deze studie niet zult denken dat het rustiger wordt. Hopelijk kunnen we samen nog veel in de ons zo geliefde *wetlands* ver-toeven.

Last but not least ook dank dat jij, Rudi Drent, al die jaren over mijn schouder hebt willen mee kijken. Vooral het zelfvertrouwen dat je me op subtiele wijze wist mee te geven was een belangrijke steun in de rug om vol te houden. In de laatste fase van de strijd heb je onze gezamenlijke koers steeds weer vorm gegeven met belangrijke correcties, hints en een goed gevoel voor *understatement.* Jouw boven-nationale denken en sublieme vermogen voor creatieve combinatie van zaken die niets met elkaar te maken leken te hebben, heeft mijn werk een enorme impuls gegeven. Ook Nel Drent wil ik

graag bedanken voor de vele *"spinach hours"* die we samen met Rudi hebben doorgebracht. Ik heb die altijd als zeer gastvrij en stimulerend beschouwd.

Het tot stand komen van een produktie als deze kan niet zonder de medewerking van velen; een cruciale rol speelde Wouter Dubbeldam bij het vervaardigen van vele "ruwe" grafieken en het telkens weer doorrekenen van nieuwe getallenreeksen. Dank, Wouter dat je werkdag niet om 16.45 h ophield als ik weer eens langskwam. Ook Dick Visser van de R.U.G. heeft op zijn betrouwbare wijze bijgedragen aan het gezicht van de wetenschappelijke illustraties, die we door jouw toedoen "artwork" zijn gaan noemen. *I greatly acknowledge the willingness of Jens Gregersen from Vorsø, Denmark to illustrate this work with his drawings which I admire so much because they reflect the atmosphere that wetland-workers have met so often but is so difficult to catch into pictures.* Ineke Touber heeft de Engelse teksten tot een eenheid gesmeed. De produktie was in handen van Henk Bos die de contacten met de drukker onderhield en de planning en kwaliteitscontrole voor zijn rekening heeft genomen.

Mennobart R. van Eerden,
Lelystad, 1 december 1997.

Chapter 1

Introduction: patch use, habitat exploitation and carrying capacity for migratory water birds in Dutch freshwater wetlands

Mennobart R. van Eerden
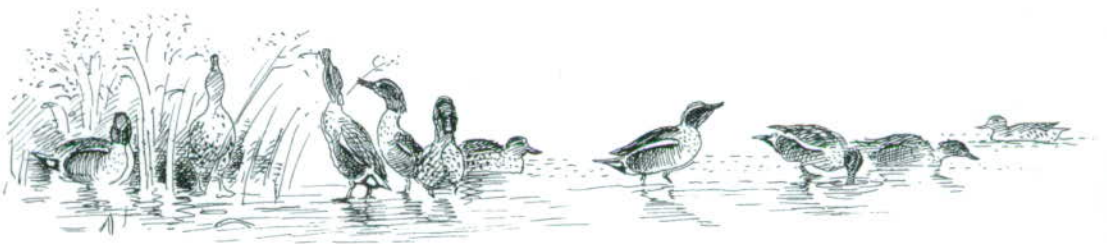
Introduction: patch use, habitat exploitation and carrying capacity for migratory water birds in Dutch freshwater wetlands

Both from a theoretical (foraging theory) and a practical (wetland development and management) point of view, insight is required how animal populations depend on their habitat.

Wetlands are considered to be threatened habitats all over the world (*e.g.* Finlayson & Moser 1991). Water birds such as ducks, geese and swans constitute an eye-catching element, relatively easy to study and representing a high natural value from the point of view of nature conservation. The biological integrity of a wetland can therefore be judged by the presence of these water birds. *Vice versa*, many species of migratory water birds completely depend on the presence of well functioning wetlands along their flyway. However, little is known about the causal background of the relationship between habitat quality and the number of animals the area can sustain, a concept often referred to as Carrying Capacity.

The aim of this work is twofold: first, to provide basic data describing food-consumer relationships for water birds in Dutch freshwater wetlands outside the breeding season and second, to compile this information, together with data from literature, into a concept which concerns food exploitation theory in relation to the issue of carrying capacity at the level of a stopover site. An *a priori* set of four lines of thought has been formulated, which is to serve as proposition statement:

1. Waterfowl populations in NW Europe may be limited by winter food supplies and not simply distributed in relation to the occurrence of strictly protected nature reserves, hence the topic has management implications.
2. Exploitation patterns of staging sites depend on patch use at different levels which relate to:
   (a) geography in relation to migration path (the flight distance - food abundance relationship)
   (b) dietary preferences (limited spectrum per site during time of use) explained by food quality
   (c) food depletion including inter-specific competition in relation to a threshold in exploitable food density
   (d) foraging costs by the consumer leading to different exploitation thresholds
   (e) other factors not considered here (hunting, disturbance, pollution).
3. Temporal and geographic exploitation patterns imply an interplay between tradition (return to reliable sites) coupled with nomadic movements to sample alternatives.
4. The creation and maintenance of a network of sustainable staging and stopover sites is necessary in an increasingly urbanised world.

Introduction

Animal numbers and food supply

The question of how animal numbers are regulated has been receiving attention for many decades (Lack 1954, 1966, Wynne Edwards 1962, 1970, Newton 1980, Sinclair 1989). Food is a necessity for every living creature and feeding ecology has therefore always played an important role in studies which deal with population regulation. In the earlier studies, the segregation of species was supposed to be the result of competition for a common resource *e.g.* food. It was not until the 1970s that the few descriptive studies included the first field experiments. Thus the long-term study on Scottish Red Grouse *Lagopus lagopus scoticus* was one of the first studies to combine the observed cyclic patterns of population development with behavioural features of the animals (Watson & Moss 1979, 1980). The condition of the heather was also taken into account, and an attempt was made to narrow down the food supply on offer in relation to the demands of the grouse into the profitable parts of their food plants (Miller *et al.* 1970).

The question of how a habitat is used also has a long tradition in science. Habitat use models have been constructed to understand the observed spatial differences in animal abundance. However, unlike foraging models, habitat research remained descriptive and rarely provided a quantitative prediction about the relation between animal abundance and habitat quality (MacArthur & Levins 1964, MacArthur & Pianka 1966, Schoener 1968).

More recently, emphasis has been laid on studies which deal with individual decision making. The way an animal behaves is considered to be not just pre-adapted to its environment, but, due to a constant selection pressure, in continual dialogue with it, aiming at a maximal achievable fitness. This view has led to a tremendous step forward and has resulted in the rapidly developing concept of foraging theory (Charnov 1976, Stephens & Krebs 1986, Maurer 1996). Based on principles which originate in economic reasoning, animals were supposed to behave along predictable lines, using information from their environment. Food can be regarded as present in distinct units, termed patches. Behavioural response to patches of different quality was considered such that the animal should maximise its long-term energy gain and, correspondingly, its fitness (see Ricklefs 1996 for review).

As in economics, a well-defined currency plays an important role in assessing the state the animal is in. Nowadays, in foraging ecology the income for the animal is often expressed as metabolisable energy per unit of time, often expressed on a daily basis (DME). On the other hand, by expending energy the animal can afford various activities (locomotion, foraging, reproduction) and may compensate for various costs such as heat loss, feather and tissue renewal). Subsequently, energetic measurements are needed to quantify the budget between DME and DEE (Daily Energy Expenditure) of the animals under study (King 1974, Drent & Daan 1980, Ricklefs 1996). Energy budgets may tell us whether birds are able to meet their demands from the food supply on offer, or have an income in excess of their current energy expenditure, which allows them to store fat for migration or later use.

Important in the context of rate maximisation was the observation that the metabolic machinery sets an upper limit to the amount of energy that can be taken up and extracted from food per day. Upper limits of DME on a sustainable basis were found to be related to the size of animal. Scaled to the level of Basal Metabolic Rate (BMR, the energy consumption of the animal at rest), maximum values of 3 to 6 times BMR (Drent & Daan 1980, Kirkwood 1983), or 7 times BMR (Weiner 1992) were found. Whether or not DME_{max} is tightly proportional to BMR (see discussion in Ricklefs 1996), the fact that per unit of time an upper limit of processable energy exists underlines the importance of time as a constraining factor which dictates the decision making of the animal. Time-related energy budgets play a decisive role in the animal's survival strategy. Sometimes time can be managed actively *e.g.* when an animal selects the most profitable food items or determines the speed of migration. In other cases the
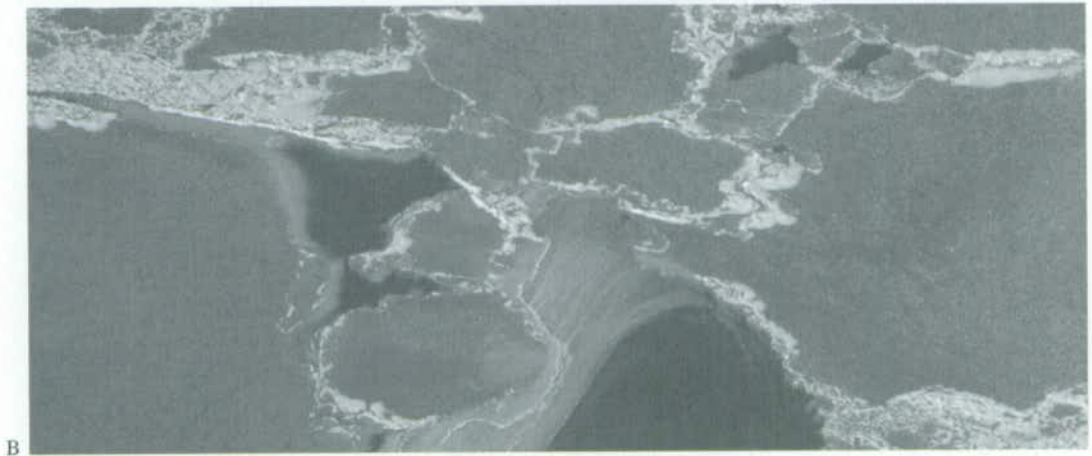
Aerial surveys are extremely useful for bird counts at large scale wetlands; lake IJsselmeer, (A) February 1991, (B,C) February 1982.

body plan dictates the speed of the process, such as the rate of food processing (gut structure) and the rate of depositing body fat. Thus, beside available energy, also time can be regarded as a major constraining factor in a foraging bird.

Carrying capacity, the number of animals that can be sustained by a certain habitat, is intuitively related to both feeding ecology and habitat quality. No wonder that the concept appeals to policy makers, land-use planners and nature conservationists. Scientifically, however, a great deal of information underlying this idea is still lacking. In studies dealing with waders in estuarine environments, John Goss-Custard has formulated the carrying capacity concept as a testable hypothesis; the carrying capacity of an area has been reached when the addition of one more animal to the habitat under study would cause the death or emigration of another (Goss-Custard 1985).

Carrying capacity

Problems concerning carrying capacity can span the range from stopover sites (10-100 km^2 and more) along an entire flyway for migratory birds (thousands of kilometres) to a single patch of food (0.01-1 m^2) within a foraging area at a given stopover site (hundreds of metres). Recently, an approach has been in demand to try to scale-up foraging patterns from food patch to habitat level, both with regard to the total amount of food used, and the consequences that limited use of food resources might have on population level (Goss-Custard 1980, Goss-Custard *et al.* 1995, 1996, Zwarts & Drent 1981, Sutherland 1996). However, remarkably few studies have measured food consumption on a larger scale, such as an entire stopover site of a migratory species, for instance.

As wetlands in the western world can be considered discrete islands in a sea of cultivated habitat, many water birds rely closely upon these sites. Already in the 1960s, the need for protecting wetlands was felt, and a network of protected areas was assembled, aiming at safeguarding the identified flyway populations (for Europe see Atkinson-Willes 1972, 1976, for North-America see Bellrose & Trudeau 1988). Migratory water birds form an important group of animals which inhabit these wetlands and, in terms of the values they represent for nature conservation, they are protected by governmental legislation and policy documents (*e.g.* under the EC Bird Directive, Bonn Convention, IUCN (1985). However, the need for studies unravelling the food-consumer relationship was acute as only a few sites offered good research facilities and, perhaps more importantly, few attempts were made by the field biologists to fill this gap. Trying to quantify food-consumer relationships at the level of an entire stopover site may seem an obvious challenge for a fieldworker, in practice it is costly and means a tremendous deal of work extending over many years. Studies on diet, consumption rates in relation to food density and the numerical response of animals to the food supply on offer need to be confronted with the quantified food stock. In many cases not the absolute food abundance, but the fraction available, or better, attainable for the animal consumers needs to be quantified. For coastal mudflat habitat and waders *Charadriiformes,* this approach has been thoroughly worked out by Leo Zwarts and co-workers (Zwarts 1996). The waders, almost entirely dependent upon invertebrate prey, possess species-specific prey detection and prey ingestion techniques, whereas the prey consistently delimit predation by an evolutionary game of hide-and-seek.

During the past twenty years I have taken up the opportunity to work along these lines in several Dutch freshwater habitats. Studies were initiated on a broad range of different species of water birds, representative of the different habitat sub-sets within a freshwater ecosystem. Much of the work has been carried out systematically, combining detailed ecological examinations with long-term counting data (10-25 years and more) and periodic habitat assessment. This period of time was felt necessary in order to allow the change in natural succession of vegetation, benthos and fish as a kind of natural experiment to which the birds were supposed to respond with a change in numbers or a different harvest level. Knowledge about processes and quantified relationships are considered useful, both for our
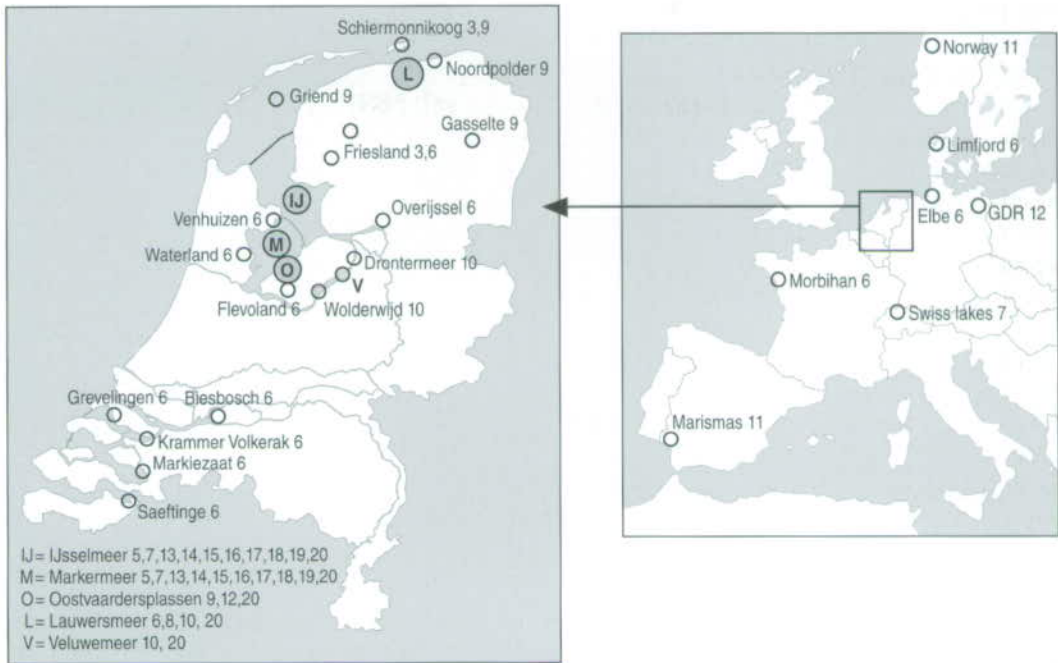
Figure 1. Study sites used to describe the food-consumer relationships of this study (shaded dots, see key). Additional study sites where samples of food were taken are shown as open dots. Numbers refer to chapters where the sites are mentioned.

understanding of how to preserve biodiversity in existing natural wetlands and for management measures in man-made wetlands.

Some of the newly created wetlands in the Netherlands were chosen as a basis for our research. Figure 1 shows the main study sites. Each site consisted of a number of typical habitat types. Nowhere was disturbance (recreation or hunting) at such a level that this could have a dominant effect on waterfowl numbers or distribution. Salt-marsh communities and brackish wet meadow systems were studied in lake Lauwersmeer, the former Lauwerszee estuary, which was embanked in 1969. Freshwater meadows and marshes were found at a scale suitable for research in the Oostvaardersplassen, a recently developed wetland in Zuid Flevoland (reclaimed in 1968). The exploitation of submerged macrophytes was studied in the Lauwersmeer and the Borderlakes of Flevoland, created in the late 1950s. At the other extreme, the lake IJsselmeer system (closed off from the sea in 1932) was chosen for comparison as it presently forms the most important large scale (c. 2000 km^2) open freshwater habitat in the Netherlands. Especially benthos and fish consumers are abundant here. These areas are described in more detail in Part III (case studies). All areas have in common that they are, in ecological terms, young of age. The production of food in this phase of natural succession is high and still bears a relation with open, dynamic natural systems of (tidal) freshwater marshes (Odum & Hoover 1988).

The basic question underlying this long-term study was how food density (quality and quantity) would affect the number and species composition of migratory birds that could use such a site. This type of information is essential if one is to manage, protect and even create new wetlands. Knowledge about the existence of possible bottle-necks in the food supply could be of help to rank priorities in decision making about management and research goals. From a scientific point of view, the relation-

ships between food density, food quality and consumers have received much attention (see for review Stephens & Krebs 1986, Carey 1996).

Two goals have been set for this study: first, to quantify food-consumer relationships in a bottom-up manner from individual patch use to an entire wetland. Second, to obtain information on the effect of trophic guild on these relationships, by combining empirical measurements from different avian groups (plant-, invertebrate- and fish-eaters).

Outline and methods

An animal requires food in order to balance its daily energy expenditure. As pointed out by Nagy (1987) extended by Nagy & Obst (1991), daily energy expenditure (DEE, kJ day^{-1}) for birds under field conditions scales to body mass as

$$DEE = 10.4 \ M^{0.67}$$

Foraging rates (F, kJ h^{-1}) also relate to body mass as found by Bryant & Westerterp (1980):

$$F = 2.02 \ M^{0.68}$$

The ratio between the two formulas represents the average amount of time a bird spends foraging, *i.e.* 5 hours. As the slope is nearly the same in both equations, time spent feeding is not related to body mass (Maurer 1996). On a mass specific basis, smaller birds consume more energy than larger birds, in absolute terms, however, the requirements of large birds are higher.

Food density is just a simple measure for what is available to a consumer and it can only provide a superficial picture of what potential carrying capacity could be. As pointed out meticulously by Leo Zwarts in his studies on waders *Charadriiformes,* the available fraction of marine benthic prey present on tidal mudflats varies according to species, time of year and even between years (*e.g.* Zwarts & Wanink 1993, Zwarts 1996). The different predators also behave differently with respect to the available fraction, which complicates generalisations about carrying capacity.

Water birds in wetlands consist of different ecological groups, which can be roughly divided into herbivores, benthivores and piscivores; energetic density of prey differs (Castro *et al.* 1989, Karasov 1996) and also costs for food provisioning vary substantially. Both parameters are considered important determinants of the bird's energy budget (Goldstein 1988, see Ricklefs 1996 for review). Water birds show a considerable variation in foraging modes with contrasting energetic costs. Diving under water while pursuing prey and flying are the most costly activities that occur in nature. Compared to standard metabolic rate, *i.e.* the amount of energy expended when an animal is at rest in the thermoneutral zone, flying and running are most expensive (up to 14 and 12 times BMR respectively, (Brackenbury 1984). Diving costs may vary between 6-7.5 times BMR for stationary divers in cold water (De Leeuw 1997) and 10 times BMR for pursuit-divers (Nagy 1984). Swimming (2.2 (slow) to 4 (fast) times BMR) and walking at slow speed (2-3 times BMR) are less costly activities for birds (Videler & Nolet 1990, Nolet *et al.* 1992, Wooley & Owen 1978). A waddling goose or a duck foraging on the water's surface requires far less energy than the costs for locomotion by a tern searching for fish in active flight or swimming under water by a pursuit diver as the Great Crested Grebe hunting for fish prey. Within one foraging guild, foraging costs may also vary. In herbivores, for instance, pecking or straining food from the water (seeds, leaves) is less costly than grubbing for roots or digging pits to extract tubers and stolons. So, it can be hypothesised that food density and quality alone do not determine the level down to which animals may harvest, but that the costs to obtain it also form an important factor.
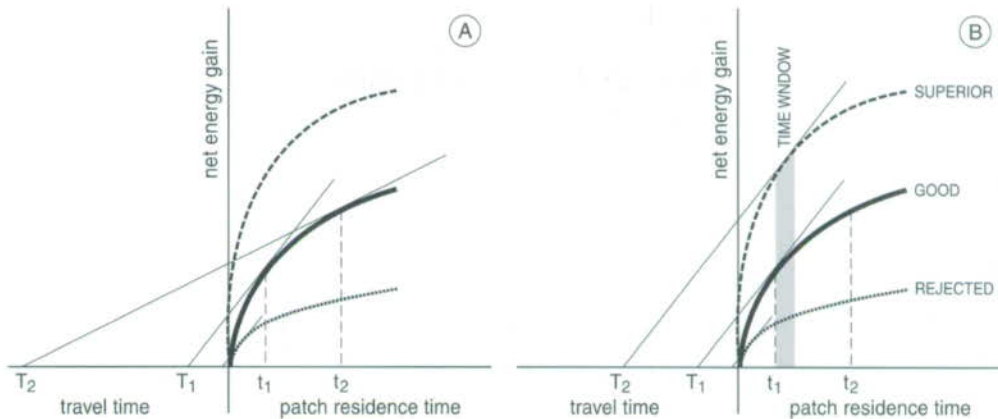
Figure 2. (A) Classic foraging theory model showing energy gain for a consumer as a function of patch residence time. If a forager has travelled longer between patches, patch residence time should increase to compensate (Marginal Value Theorem, Charnov 1976, see Stephens & Krebs 1986, their Chapter 2, p. 30). The optimal solution for patch exploitation time is found by constructing the tangent to the gain curve. (B) As an extension to the theory now consider a stopover site as a huge food patch and patch residence time fixed, as in a migratory bird with a narrow time table. It then follows that rich sites would attract birds from a longer distance, whilst others are unattractive. In this figure, equal rewards (intake over time) are offered to the long distance migrant (T_2) compared to the short distance migrant (T_1).

Figure 2 shows a qualitative model of the expected relationships between foraging costs, energetic return and patch harvest level. It is based on the classic foraging models used to describe patch leaving decisions in relation to time spent travelling between patches (Ydenberg 1984, Stephens & Krebs 1986: Chapter 2). As an extension to these models, foraging efforts and energetic gain for different food types were considered to operate at a higher level than the single food patch. It is assumed that feeding conditions at a stopover site as a whole can be considered a "super patch", as compared to other halting sites along the birds' flyway. Time spent in such a super patch would thus not only depend upon the amount and quality of the food present, but also on the conditions elsewhere. In particular, questions as to timing of migration and duration of stay at a stopover site could be evaluated, if flight distance between stopover sites is considered as travel time between patches. Analogous to the classic theory, a bird thus would aim to stay longer at a site when the travel distance from the previous haunt was longer (Fig. 2A). Also, if the quality of a site on the flyway level in terms of available food increases, this site would attract birds from a greater distance (Fig. 2B).

As stated before, situations with measurable food densities at field scale are rare. In the Netherlands, the struggle against the water has a tradition of at least a 1000 years (Schultz 1992). The more recently reclaimed polders and dammed estuaries provided good research possibilities for the purpose of our study. Often left alone for many years before cultivation could be started, and sometimes designated as nature area, when protection against the sea was the only purpose, natural succession could go on undisturbed. Food for water birds was abundant and comprised often single or a few species. Natural succession caused food density to change dramatically at a rate which was manageable by the researcher (10-25 years). The complete turn-over from one ecosystem to another provided excellent starting conditions to study the effect of a new territory on the numbers of migratory water birds. As such, I have considered the biological processes during the making of polders or the damming up of estuaries as large scale natural experiments, useful for studying the process of colonisation by food organisms and their consumers.

Gradient-rich freshwater habitat provides many feeding opportunities for water birds. Oostvaardersplassen, August 1987.

Impact estimates were determined in the field and taken from literature. The ideal route to study carrying capacity problems is to monitor biological processes in nature, and to carry out experiments both in nature and under controlled (semi) laboratory conditions. Such an integrated study has recently been published as a companion volume on the ecological energetics of wintering diving ducks (De Leeuw 1997). In undertaking this study, two major objectives were kept in mind.

First, to investigate the direct relationship between food availability and response (numerical, functional) or impact (patch harvest level at different levels of scale) by the consumer. The basic idea is that, because costs for foraging differ greatly among the ecological groups under study, as does the energy content of the food, food harvest levels may vary according to the net energy gain per unit of time (gross intake rate minus costs required for foraging, digestion and other losses). Figure 3 shows the expected relationships in a graphical way (see also Stephens & Krebs 1988). If foraging costs increase, patch residence time becomes longer and patch harvest level increases. The aim was to test this hypothesis and to derive a conceptual model for carrying capacity issues of natural areas.

Second, by combining results from herbivore, benthivore and piscivore representatives of the group of water birds, all belonging to a few families of birds and often assembled in the same wetlands, I will attempt to construct an overall picture of the key parameters that determine carrying capacity with respect to food provisioning in relation with the feeding style. As the scope of this study is wide, it can not be expected that tailor-made solutions can be achieved for all ecological groups. As an example, the integrated diving duck study mentioned earlier took c. 15 man-years (De Leeuw 1997).

In view of the above, it may be good to state where this work is *not* about. Not studied are, for instance, the various sources of disturbance (hunting, recreation, traffic), factors which also affect carrying capacity, and the effects of pollution and pesticides limiting bird numbers. However, these factors played no significant role in the cases described here.

The contents of this work can be divided into four parts: Background, Constraints, Case studies and Evaluation.
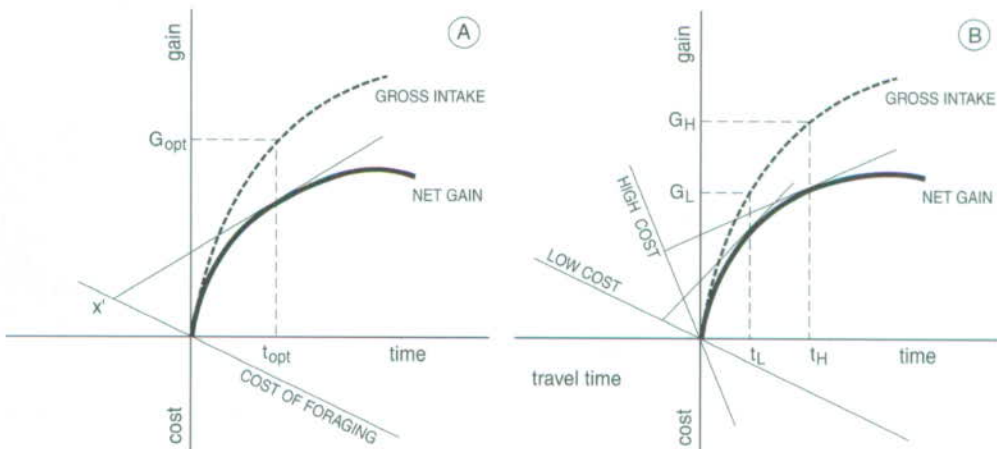
Figure 3. Model describing optimal patch residence time including foraging costs. In extension to Figure 2, gross and net intake gain curves have been drawn. Note that the optimal solution is found by constructing the tangent to the net gain curve, whereafter the gross gain is derived. The costs of foraging are subtracted from the net energy gain by rotating the abcissa and drawing the tangent from x^1. (A) Energy costs for travel and foraging are the same. (B) Higher travelling costs imply longer patch residence time and a higher energy gain. Modified after Stephens & Krebs (1988).

Part I: Background and terms of reference

To put the current situation of wetland abundance in the Netherlands in a wider perspective, the first two chapters deal with the past. Chapter 2 describes the historical situation in the Netherlands, starting 7000 years ago. Due to climatic change and reinforced by influences by man, the original realm of sheer endless wetlands finally became narrowed down into well-defined super patches of protected nature areas. The consequences of this large-scale impoverishment for water birds are being discussed, and a tent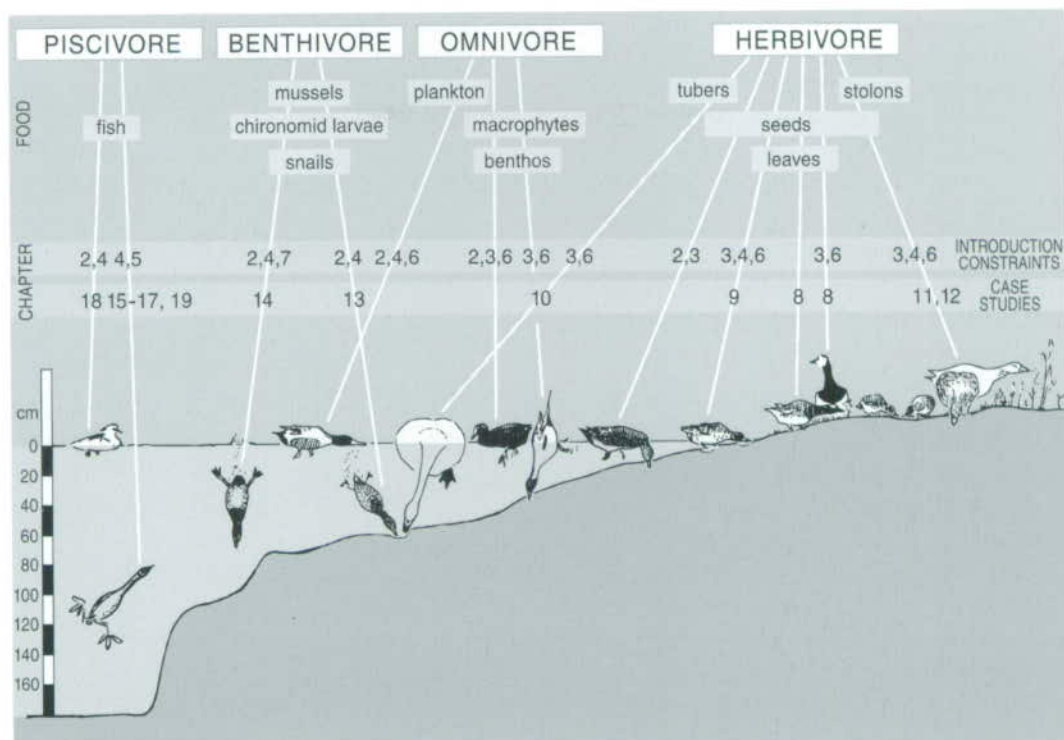ative exploration is made of the quantitative consequences of the continual habitat shift. Chapter 3 concentrates on the impressive changes in land-use that have occurred in the last two centuries. Due to agricultural changes, the carrying capacity for wintering herbivorous ducks, geese and swans has greatly improved on farmland, while natural habitats suffered an accelerated degradation. We address the question whether the winter food-bottleneck of this group has been released by the improved quality and quantity of a variety of cultivars providing enormous amounts of seeds, roots and protein-rich leaves.

Part II: Constraints

Wintering water birds are confronted with rapidly changing conditions while on migration and in their winter territories. Having spent the summer in their northern, mostly undisturbed breeding grounds, they migrate towards the south with their young. The range from which birds reach the Netherlands extends from NE Canada for some waders and geese, via Spitsbergen and Scandinavia eastwards to Russia, far behind the Ural mountains. Two events require special attention following the breading period. First, moult of wing feathers imposes in many water birds a constraint on their movement. Being flightless for several weeks (3-5 depending on size of the species), a habitat is selected which must meet conditions of safety and food availability. Second, prior to the period of wintering, fat deposits are usually laid down and this entails special demands on the birds' energy requirements. Stopover sites are often used to replenish fat reserves needed for further migration (Alerstam & Lindström 1990).

During winter itself, many water birds are fully dependent upon the aquatic habitat. Being exposed to contact with water, the whole or part of the day, Chapter 4 explores the costs for maintaining body temperature as a function of body mass and degree of contact with water. Heat transport between the bird and its environment was measured using dead birds with intact plumage. The predictions about energy expenditure, earlier derived from thermal conductance studies using dead birds, was tested in a study on Great Crested Grebes (Chapter 5). These birds were freshly collected after having drowned while foraging in gill-nets of fishermen. Using a sample of over 1300 birds, daily food intake was estimated from gut analysis. The possible increase of food intake as a function of decreasing water temperature was thus investigated under field conditions.

Beside constraints imposed by the environment, the animals face costs for digestion of their food. This is especially the case for bulk eaters, such as avian herbivores and some benthivores which ingest entire shells. Not only food selection and intake rates, but digestion capacity of the gut sets the limit of food processing in those cases (*e.g.* Karasov 1996). Herbivorous water birds, *i.e.* a large group of ducks, geese and swans, can only superficially digest plant food. We investigated whether food availability *per se* or the capacity of the gut to digest, could set the major limit to habitat selection and food choice. Chapter 6 combines field data on digestibility of naturally taken food and an estimated energy return is quantified. Using data from a variety of species, we related apparent digestibility to body size. In the course of our trials we studied a mass range from 300-12 000 g exists, thus spanning the entire range in body mass of this group of birds in the western Palearctic. It is expected that the smaller species will have to be more selective (and thus be more susceptible to changes in quality of their habitat) in order to meet their daily energy requirements. Some food sources may not be exploitable

PISCIVORE | BENTHIVORE | OMNIVORE | HERBIVORE

FOOD

		mussels	plankton		tubers		stolons
fish		chironomid larvae	macrophytes			seeds	
		snails	benthos			leaves	

CHAPTER

| 2,4 4,5 | 2,4,7 | 2,4 2,4,6 | 2,3,6 3,6 3,6 | 2,3 3,4,6 | 3,6 | 3,4,6 | INTRODUCTION CONSTRAINTS |
| 18 15-17, 19 | 14 | 13 | 10 | 9 | 8 8 | 11,12 | CASE STUDIES |

cm
0
20
40
60
80
100
120
140
160

Figure 4. Schematic cross-section through a freshwater wetland with typical avian consumers belonging to different foraging guilds. The numbers refer to chapters where the species are described.

because of a too low energy content, others because the intake rate can not be maintained at the right level.

In Chapter 7 the ultimate effect of low food stocks in relation to harsh weather conditions is described. A mass die-off of diving ducks, which took place simultaneously in Switzerland and the Netherlands, was examined. Harsh weather conditions, in conjunction with low body condition of the birds and low food availability may have been reasons for this to happen.

Part III: Case studies

The next twelve chapters are devoted to case studies, describing different food-consumer relationships, in most cases measured under field conditions. Where possible, field experiments were conducted supported by feeding trials carried out with birds in captivity. The chapters are divided into three sections according to the type of food involved. Plants, bottom-fauna and fish were chosen as distinct groups in which issues such as foraging behaviour, consumption rates and harvestable fraction were determined.

How birds exploit food was best studied in herbivores. This group offered the best opportunities to collect detailed data on patch use, at levels between a single food patch of 100 cm^2 and an entire stopover site of 10 000 ha. A selection of 5 typical cases was made to illustrate the basic findings for this group. Benthos-feeders were studied at lake IJsselmeer and two chapters are devoted to the ecological description of the system and its benthos consumers. The fish-eaters among the avian con-

sumers consist of a heterogeneous group. Like benthos feeders they dive for food, but in most cases a pursuit dive is made because their prey is mobile. In this group specific problems like underwater visibility impose extra constraints on prey catchability. Using data from the large IJsselmeer system, factors such as sex, age and social foraging are described in the context of feeding ecology in a comparative way. In no other group of water birds is the segregation between the different categories within one species so apparent. We used this knowledge to test hypotheses about prey exploitation among fish-eaters.

Figure 4 gives an overview of the different ecological groups of water birds studied. Beside the schematic positioning along an imaginary cross-section of a wetland, the chapters in which the species are dealt with are indicated.

Herbivores

Avian herbivores can often be studied during daytime and food analysis is relatively easy because of the poor digestibility of the cell wall of their food plants. Microscopical determination of cell fragments reveals a good insight in diet composition (Owen 1975). Direct observation of the vegetation may also provide details about the species and plant parts consumed. Chapter 8 outlines the general ideas of the concept of the flyway and patch use down to the level of a single food patch in the field. The huge supplies of *Salicornia* on the former sea bottom, which has changed over the years, provided a unique chance to study food-consumer relationships at different scale levels.

Chapter 9 explores in detail how in an experimental set-up Teal *Anas crecca* choose among patches with different seed density. A variety of seed species was tested as to intake rate and preference in relation to structure of the seed coat. The influence of indigestible debris particles on seed consumption was also studied as these impurities often occur in the natural situation. By scoring the sequence of patch use in relation to the simultaneously derived intake rate, the decision pattern of the birds could be analysed. As in nature, ducks must continually decide where to go, how long to stay and what to select in a certain food patch. We tried to determine which information about food supply is used by the ducks and how discrimination among patches takes place.

Chapter 10 also considers patch use, but then in the field and at various levels for wild Bewick's Swans *Cygnus columbianus bewickii*. During autumn migration these birds largely depend on the storage organs of water plants, the tubers of Sago Pondweed *Potamogeton pectinatus*. Patch exploitation patterns were analysed using data over many different years for lake Lauwersmeer as well as the Borderlakes in Flevoland. Initial density in relation to water depth and soil type, but also annual differences were important for explaining the observed patch harvest levels. By combining the autumn sampling data with the summer mapping of vegetation density through aerial photography, a lake-wide survey of available tuber stock could be obtained, which could be compared each year with the swans' use of the area. When they reach the Netherlands, Bewick's Swans have almost come to the end of their autumn migration. Closely related to this question, Chapter 11 describes food exploitation in another herbivore, the Greylag Goose *Anser anser*. The geese use the same area, lake Lauwersmeer, as the swans, but in their case as a stopover site during autumn on their way from Norway to central and southern Spain. During their stay the geese use terrestrial food in the form of grass seeds which they strip off the ears. The questions about patch use, food selection and carrying capacity of the entire site are again considered in relation with the annual rhythm of the geese. One of the questions was whether the birds use the principle of time minimisation (to cover the migratory range as fast as possible) or energy maximisation (to achieve and maintain the best condition at the stopover site), and whether this could explain food choice and harvest levels at the halting place (Alerstam & Lindström 1990). Trials with captive geese were used to determine possible alternatives of food choice available to the wild geese as well.

In Chapter 12, Greylags are again described, when temporarily concentrating in a freshwater marsh

during their annual wing moult. Tens of thousands of geese cause massive defoliation of tall reed stems during the several weeks of their natural captivity, which is their flightless period (38 days). The seasonal harvest pattern and the constraints caused by the poor and even declining digestibility of reed are analysed against the background of the modification of the available food supply as a result of heavy annual grazing. It is discussed how the impact of herbivores can affect the long-term survival of their food plants.

Benthivores

Two chapters deal with benthivorous diving ducks at lake IJsselmeer. This freshwater system was chosen because of its international importance for diving ducks and the relative simplicity of the food chain. Diving ducks of the genus *Aythya, Bucephala* and the Coot *Fulica atra* make dives to the bottom of the water they exploit. With their bill they grasp prey attached on substrates, or dig shallow pits or strain food from the top soil layer. Chapter 13 explores which factors determine the availability of Zebra Mussels *Dreissena polymorpha,* the main prey for diving ducks in lake IJsselmeer. Unlike the often hidden prey of waders on tidal mudflats, *Dreissena* living on the lake bottom seems easy to catch. Spatial and temporal variation in the strength of byssal attachment were considered as well as measurements on condition of the mussels. Profitability of different mussels was tested using a semi-natural diving device with automatic dive recording. Chapter 14 describes the use that wild diving ducks make of the area. Long-term monthly aerial counts and two lake-wide surveys of the stock of mussels provided the background for the analysis of habitat use by the ducks (radar studies, distribution of drowned ducks) and feeding behaviour (food analysis by inspection of the guts of birds caught in fish-nets while foraging, impact assessment of fixed plots).

Piscivores

Fish-eating birds were studied at lake IJsselmeer, the same lake system where the research of the diving ducks took place. Chapter 15 enlightens the constraints on prey availability for pursuit divers imposed by underwater light climate. During wing moult, Great Crested Grebes gather by thousands close to the shore of the lake. Detailed records of the distribution of Smelt (echo-sounding, beamtrawl catches), the main prey of Great Crested Grebes *Podiceps cristatus*, were made both with respect to temporal (seasonal, annual) and spatial (water column) variation. From the abundance of co-occurring Perch *Perca fluviatilis,* fish predators on the same prey, we tried to assess the impact by the grebes and the extent of the competition between avian and fish predators (Chapter 16).

Great Crested Grebes were again studied with respect to prey choice in winter time, when water temperatures are low. Grebes are then dispersed over vast areas and many of them have left the area. By describing the diet of over 1300 freshly caught grebes (gill-nets of commercial fishermen), the constraints on prey availability are further explored in Chapter 17. Water temperature and underwater light climate were considered factors of prime importance within this respect.

In contrast with the grebes, which are solitary hunters, we turned to another species to study the effect of social behaviour on fish attainability. Chapter 18 deals with Smew *Mergus albellus* exploiting Smelt. Again underwater light climate, prey abundance and the behaviour of the predators constituted the triangular unity which determined prey availability. Social behaviour as was observed during flock hunting was expected to enhance prey availability in turbid waters.

Finally, Chapter 19 describes food choice by Red-breasted Mergansers *Mergus serrator.* These birds, which are sexually highly dimorphic, were described in relation to the question of how structural size, through an imposed limit in energy expenditure, would affect prey attainability.

Part IV: Evaluation and synthesis

In this chapter all knowledge obtained in the previous chapters is brought together, and combined with data taken from literature. The factors which determine Carrying Capacity, can be divided into two parts: (1) consumer-based factors: body size, "Bauplan", degree of water contact, trophic level of inter-action, and (2) environment-based factors: food quality and food availability. The maximum work capacity of a bird and the general time constraint to achieve the necessary income in terms of metabolised energy are considered a major reference for the evaluation (Hammond & Diamond 1997).

Attempts are made to derive specific points of focus in relation to wetland management. As the environmentally based factors are manageable and the predator based are not, directives for nature development should aim at the former. Breaking down the comprehensive issue of the carrying capac-ity of staging areas into workable sub-issues, I have come to the following four key questions, based on *a priori* hypotheses concerning carrying capacity for water birds in freshwater wetlands outside the breeding season.

1) Does knowledge of net food intake rate in relation to daily metabolisable energy required, help to explain patch harvest levels in a depletion scenario?
2) To what extent may foraging costs of the consumer and energetic return of food determine harvest levels and thus carrying capacity?
3) Is it possible to scale-up patch use patterns to higher levels (area or zone, stopover site along the fly-way) which would allow predictions about carrying capacity of the area?
4) How do other factors such as the migratory time-table, in relation to the annual rhythm of the con-sumer, additionally determine local patch harvest levels?

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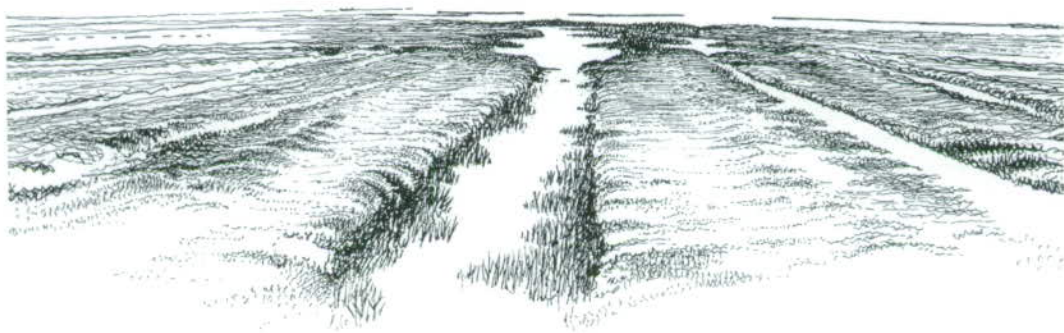
Chapter 2

Long-term changes in wetland area and composition in the Netherlands affecting the carrying capacity for wintering water birds

Mennobart R. van Eerden, Gerda Lenselink & Menno Zijlstra

Long-term changes in wetland area and composition in the Netherlands affecting the carrying capacity for wintering water birds

In the Netherlands, arising in geological time as the delta of the rivers Rhine, Meuse and Scheldt, a considerable change in landscape occurred during the Holocene period due to sea level rise. In more recent times this change was dramatically enforced by the actions of Man. This started with the opening up of the large woods on higher soils, some 4500 years BP. It is estimated that the country was only populated then by a few thousand people. During the next 2000 years, the extensive forest clearing continued, and up to approximately 60% of the upland area changed into grazed woodland. Over-exploitation during the Middle Ages resulted in extended heathlands, which covered up to 40% of the total area of upland sands by 1500 AD. Today woodlands cover only 1 promille of the surface area it covered 7000 years ago. Wetlands remained undisturbed for a long period, but they have become seriously affected since the late Middle Ages; the construction of dikes, embankments and drainage have caused the area of wetlands to shrink dramatically. Especially when in the 19th and 20th centuries, as a result of the introduction of steam and later diesel and electric engines, large-scale projects could be realised. This led to the disappearance of many freshwater lakes and the almost complete loss of the area of brackish water, the natural link between sea water and freshwater. Although the influence of Man upon the Dutch landscape commenced some 4500 years ago, it is only during the last 600 years that wetlands have been affected. Particularly the last 100 years have been crucial with respect to drainage and cultivation.

By reconstructing ancient landscapes, an attempt has been made to describe the species composition and numerical abundance of water birds, starting 7000 years BP. Two species have become extinct in the territory, many others show changes in abundance. The start of agriculture has caused a major change in the food provisioning of many herbivorous water birds. Over the last 7000 years, a sevenfold increase of the number of herbivorous waterfowl is estimated. On the other hand the number of fish-eaters, benthos-eaters and planktivorous water birds has declined, their available habitat now having diminished by 45%, 36% and 55% respectively with respect to the Late Subatlantic period, *c.* 850-1350 AD.

Introduction

As delta of the rivers Rhine, Meuse and Scheldt the Netherlands has always been a territory where the link between water and land has been an important feature. Wetlands have presently changed compared to the situation of 7000 BP. In general, climatic changes after the last glaciation, which ended about 10 000 years ago, have caused the sea level to rise and have affected the shoreline and the course and water discharge of the large rivers, as well as the vegetation. Moreover, the human impact upon the landscape has greatly influenced the extent to which natural fluctuations of water tables occur.

This paper aims to describe the general change in landscape and habitat diversity that has occurred over the last 7000 years, in order to evaluate the present-day situation. Our approach was to combine

information from palaeo-geographical, socio-economical and biological databases. The role of Man in changing the wetland communities will be emphasised, focusing upon the period from 850 AD until the present. The present situation will be evaluated with respect to habitat diversity, degree of natural processes and possible changes in carrying capacity for water birds.

Water birds (divers, grebes, cormorants, ducks, swans, geese and rails) were chosen as they constitute a well-documented element of the wetlands, and are often used to illustrate the importance of these areas. By their highly mobile life-style they are able to respond quickly to changes in habitat quality.

A better understanding of the situation in the past is important with respect to the goals for integrated water management (Ministry of Transport, Public Works & Water Management 1989), nature conservation and the possible line of development and/or the restoration of (parts of) the original situation (Ministry of Agriculture, Nature Management and Fisheries 1990). This knowledge is also useful in order to reconstruct possible ancient migration systems in water birds (Hale 1984, Piersma 1994).

Methods

Palaeo-geographical maps

Basic information about landscape development was derived from the literature, supplemented by unpublished material for the IJsselmeer area. For this project, a new series of palaeo-geographical maps of the Netherlands has been compiled. The most important sources were the palaeo-geographic reconstructions of the prehistoric environment made by Zagwijn (1986, scale 1:1 500 000). This series of ten maps is based on data from published and sometimes unpublished material from the Geological Survey. Since then, as a result of the joint project 'Coastal Genesis' of the Geological Survey of the Netherlands and the Ministry of Transport, Public Works and Water Management, a large amount of new data has become available, especially for the coastal areas (Van de Valk 1992, Van der Spek 1994). In the intervening years, over twenty thousand cores, gathered since the early twenties on behalf of the Zuiderzee-project, have also been interpreted by Rijkswaterstaat Directorate Flevoland (and its successor Directorate IJsselmeergebied), which has resulted in revised landscape reconstructions for the IJsselmeer area. Together with the updated maps on coastal areas, they form the basis of a new series of six palaeo-geographical reconstructions for the IJsselmeer area, the province of Noord Holland and a part of Zuid Holland (Lenselink & Koopstra 1994, 1:250 000).

These three data sets together have been incorporated in the new series of six palaeo-geographical maps for the entire country. For this purpose Zagwijn's palaeo-geographical reconstructions, published at 1:1 500 000, and the reconstructions of the prehistoric environment by Lenselink & Koopstra 1994, published at 1:250 000, were digitised in the Geographical Information System ARC/INFO and pragmatically linked (Table 1). No attempts have been made yet to make the polygons fit exactly, but the minor discrepancies apparent upon close examination of our images do not affect our area-wise reconstructions. Both maps with their differences in scale and geographical imperfections were supposed to be best represented when still identifiable in the newly compiled series.

To tune the legend description of the different palaeo-geographical maps, generalisations have been made resulting in the following legend: open water, pleistocene sand areas (originally afforested areas), tidal flats, saltmarshes and mudflats, peat (divided into fen-peat and raised bogs), riverine deposits and dunes and beach barriers.

For the present situation the land use database of the Netherlands (LGN-2 database, Staring Centrum, 1994) has been used and modified into a map with a simplified legend. The land use map of the present situation, based at 1:50 000 was generalised to 1:250 000.

To show the degree of Man's influence on the landscape in more detail, for the IJsselmeer region

Table 1. Compilation of a new series of palaeo-geographical maps for the Netherlands derived from different sources (see Fig. 1). LGN = Landgebruik Nederland, database of land use in the Netherlands, Staring Centrum.).

Source	Zagwijn (1986) (C[14] years ago)	Lenselink & Koopstra (1994)	LGN-2 (1994)	This paper
2:	7000	7000 BP		A Early Atlantic, 7000 BP
3:	5300	5500 BP		B Late Atlantic, 5500 BP
5:	3700	3700 BP		C Middle Subboreal, 3700 BP
7:	2300-2100	2100 BP		D Early Subatlantic, 2100 BP
9:	500-700	850 AD		E Middle Subatlantic, 850 AD
10:	1000-1200	1350 AD		F Late Subatlantic, 1350 AD
	Recent	1993 AD	1993 AD	G Recent, 1993 AD

during the last millenium a series of land use maps has been compiled. The maps focus on the degree in which landscape forming processes occur naturally.

Landscape units as habitat for water birds

For each map an estimate was made concerning water depth (0-2 m, 2-5 m and deeper) as well as salt content (fresh, brackish and saltwater), based on the course and extent of the river flow and the dimension and estimated depth of the ancient lagoons and lake systems. We used information from malacofauna remains in the soil layers and where no information was available, a crude estimate was made by judging the effluent of the streams and rivers as well as the distance and width of the connection (if present) to the sea. Sea water, important for seaducks and divers, was considered present in a stretch of *c.* 10 km outside the beach barrier in the Early Atlantic. For ease of comparison, this boundary was kept constant during all later periods.

From data of land use in Louwe Kooijmans (1995), the following habitat types were added: afforested land, grassland and arable land. The latter, Man-induced habitats were established primarily on the drier pleistocene soils and riverine deposits according to Louwe Kooijmans (1995). The recently forwarded view by Vera (1997) that the primeval vegetation of the lowlands of western and central Europe was not a closed forest but a park-like landscape in which woodlots are interspersed with grasslands, does not affect our study on the effects on waterfowl. Neither pristine climax forests nor semi-open landscapes with tall grasses and herbs form an important habitat for this group. Only in historical times (after 1350 AD) became wetlands also drained and developed for agricultural purposes.

Based on soil characteristics, marshes were divided into sandy, peaty and clayey categories. To get a crude figure, we estimated that at least 5% of the area of dunes and beach barriers and 10% of the area of heathland consisted of this wet type (water at the surface in winter). Similarly, clay marshes were approximated as occupying 2% of the freshwater area (soil dependent) and 2% of the brackish waters.

In order to describe the animal abundance in the past, we used the partitioning in landscape types as a basic measure. Information about bird density was derived from recent inventories in comparable landscapes in the Netherlands (coastal area: Baptist & Wolf 1993, Camphuysen & Leopold 1994; estuarine and delta habitat: Meininger *et al.*, 1984, 1985, 1994, Meininger & Van Haperen 1988, Meire *et al.* 1989; Wadden Sea: Smit & Wolff 1981, Zegers & Kwint 1992, Meltofte *et al.* 1994; freshwater wetlands (clayey and sandy soils: Lauwersmeer, Oostvaardersplassen, IJsselmeer, Markermeer, Flevoland): De Leeuw & Van Eerden 1995, Van Eerden 1985, Van Eerden & Bij de Vaate 1984, Van Eerden & Zijlstra 1986, Van Eerden *et al.* 1995, unpubl. data; riverine wetland habitat (Rhine, Waal, IJssel and

Meuse): Van den Bergh *et al.* 1979, (Meuse in Limburg): Van Noorden 1992; fen-peats (NW Overijs-
sel): SOVON, M. Van Roomen *in lit.*, pers. obs. MRE; raised bogs (Fochteloërveen, Bargerveen and
adjacent areas in Niedersachsen): SOVON *in lit.*, pers. obs. MRE). Additionally, literature data from
neighbouring countries were used: coastal sites in Schleswig Holstein, Germany (Petersen 1987) and
Denmark (Joensen 1974, Meltofte 1988, Laursen *et al.* 1997), raised bogs in Jutland (J. Gregersen pers.
comm.).

Two estimates of abundance of water birds were used to reconstruct a crude pattern of bird abun-
dance in the past. Average winter (Nov.-Feb.) density was taken as to represent the significance of the
Dutch territory as winter habitat. Also, the maximum numbers per habitat were used although they are
difficult to extrapolate to the much larger areas of the past and may easily lead to over-estimation. Peak
numbers can occur if other factors are not limiting bird numbers, such as capacity of the breeding areas
or, more likely, the wintering areas. As agriculture played a far less prominent role in the past, it is
likely that the winter food bottle-neck will have been set by the presence of natural foods (see Chapter
3, Van Eerden *et al.* 1996). Therefore, the use of natural habitats by (merely herbivorous) water birds
at maximum density during the peak of exploitation (mainly in autumn) is only possible if elsewhere
on the flyway enough winter capacity would exist. We assume here that this was the case further to the
west and south-west to the Netherlands.

The GIS maps were used to calculate surface areas of the different landscapes. Subsequently, bird
numbers per landscape unit were calculated. The sum of the different habitat types gave an estimate for
the average total population present.

In order to assign bird densities in the ancient landscape types as accurately as possible, we used a
maximum estimate (100% of the area available to the birds) and a lower estimate (only a fraction of the
habitat available). For example, fen-peats are partly afforested or covered with rough shrubs not suit-
able for water birds. The fractions applied to arrive at the lower estimate were: fen-peat (30%), raised
bog (15%), river deposits (30%), saltmarshes (60%), tidal flats (80%), grassland and arable land dur-
ing the past (60%), idem recent (20%). The fractions differ according to estimated percentage of water
on surface and the proportion of vegetation cover suitable for bird use. The latter "best educated
guesses" are based on today's knowledge of larger-scale habitats still present in Europe.

Results

Palaeo-geographical reconstruction
The change in landscape and physio-geographical characteristics of the Netherlands has been depicted
in six maps (Fig. 1). The different periods are briefly described below.

1. An impressive rise of sea level (10 000 - 7000 BP)
About ten thousand years ago, at the transition of the last pleistocene glaciation to the holocene period,
the sea level was at least 45 m lower than today (Jelgersma 1980). The Dutch landscape in this period
can be described as an undulating sandy landscape. By this time the climatic changes *e.g.* the temper-
ature rise took place very quickly, and within 2000 years enough ice had melted to let the sea level rise
to about 25 m below Dutch Ordnance Level (NAP).The southern part of the North Sea area became
flooded and the sea penetrated valleys in the western part and, at a smaller scale, in the northern part of
the Netherlands. Water tables started to rise and the succession of the prevailing vegetation of pine for-
est into deciduous forests may have depressed evapo-transpiration (Zagwijn 1986, Pons 1992). The
milder climate greatly stimulated the vegetation growth. Around 8000 BP peat developed in small
brooklets and in the area between the saltmarshes and the higher pleistocene areas.

In the following millennium the sea level rose again by about 10 m, so that around 7000 BP the coastline was situated about 10 km outside the present Dutch coast line.

2. An extensive lagoon complex (7000 BP - 5500 BP)

Around 7000 years ago, the western part of the Netherlands was marked by an extensive lagoon as well as tidal flats and saltmarshes that covered the oldest peatlands. This lagoon in "Northern Holland" and its hinterland "the IJsselmeer area" was situated in an abandoned pleistocene valley of the river Rhine. Small rivers drained the fringing pleistocene sand area over gently sloping surfaces to the west. Sediment supply was largely lacking and fresh water supply was limited to the discharge of superfluous rainfall. In a calm environment, sedimentation of brackish lagoon clays took place (with typical brackish water fauna). Outside the lagoon, due to the deterioration of natural drainage conditions as a consequence of sea level rise, peat developed at the lowest parts (up to 9 meter below NAP) of this afforested pleistocene cover-sand area.

From 7000 to 5500 BP, the sea level rose further to 6 to 4 m below NAP. This caused an expansion of the lagoon to the east where it reached its greatest size about 5000 years ago. Marshes and mudflats developed and constituted an important part of the actual coastal area. Large forests in the pleistocene areas were flooded and reduced the total surface covered with forest from 70% to a mere 50%. Fens spread and shifted progressively inland and upward both in the IJsselmeer area and the area around the Frisian Middelzee. At the end of this period the peatlands covered more than 10% of the total surface of the Netherlands.

The riverine area about 7000 years ago formed only a few percent of the total surface. Its extent was determined mainly by the discharge of the rivers Rhine and Meuse. At this period there was no significant sedimentation in the floodplain. With the increase of poor drainage conditions and the sea level rise, this floodplain area extended. Considerable clay deposits formed and peat growth started locally.

There is neither evidence nor suspicion of human influence on landscape development at that time. Only a few thousand people lived here, especially in the pleistocene afforested areas, and they were hunters, fishermen and gatherers making use of the natural resources (Van Es *et al.* 1988, Louwe Kooijmans 1995). All habitats can still be considered natural.

3. Extended peatland formation (5500 BP - 3700 BP)

With the slowing down of the sea level rise to less than 2 mm per year, coastal barriers developed more strongly and closed off the coast almost completely. Due to strong protection by these barriers the former brackish lagoon became more fresh, which created optimal conditions for further peat growth. The "IJsselmeer area" and nearly the entire coastal plain, including the tidally influenced lower floodplain of the rivers Scheldt, Meuse and Rhine, were transformed in less than 2000 years into extensive peatlands which occupied more than one third of the total surface. Outside the areas under direct influence of the rivers and brooklets, reed marshes (or fens) may have turned into mesotrophic fens and carrs and developed into bogs and raised bog complexes. A mosaic of fens and raised bogs characterised the coastal zone (Pons 1992).

Small streams such as the river IJssel were not able to maintain their individual outlets to the sea. The courses in the coastal areas were closed off and the river IJssel started to discharge into a lake; one of the early stages of the lake Flevo.

Tidal flats and saltmarshes only continued in the northern part of the country and at the outlets of the main rivers. Because of the formation of coastal barriers, the total area influenced by sea or brackish water was reduced from about 25% in 5500 BP to less than 6% in 3700 BP.

In this period, people still preferred the higher pleistocene areas to live. The introduction of farming resulted in the opening up of the forest for settlements and arable land (shifting cultivation); cattle
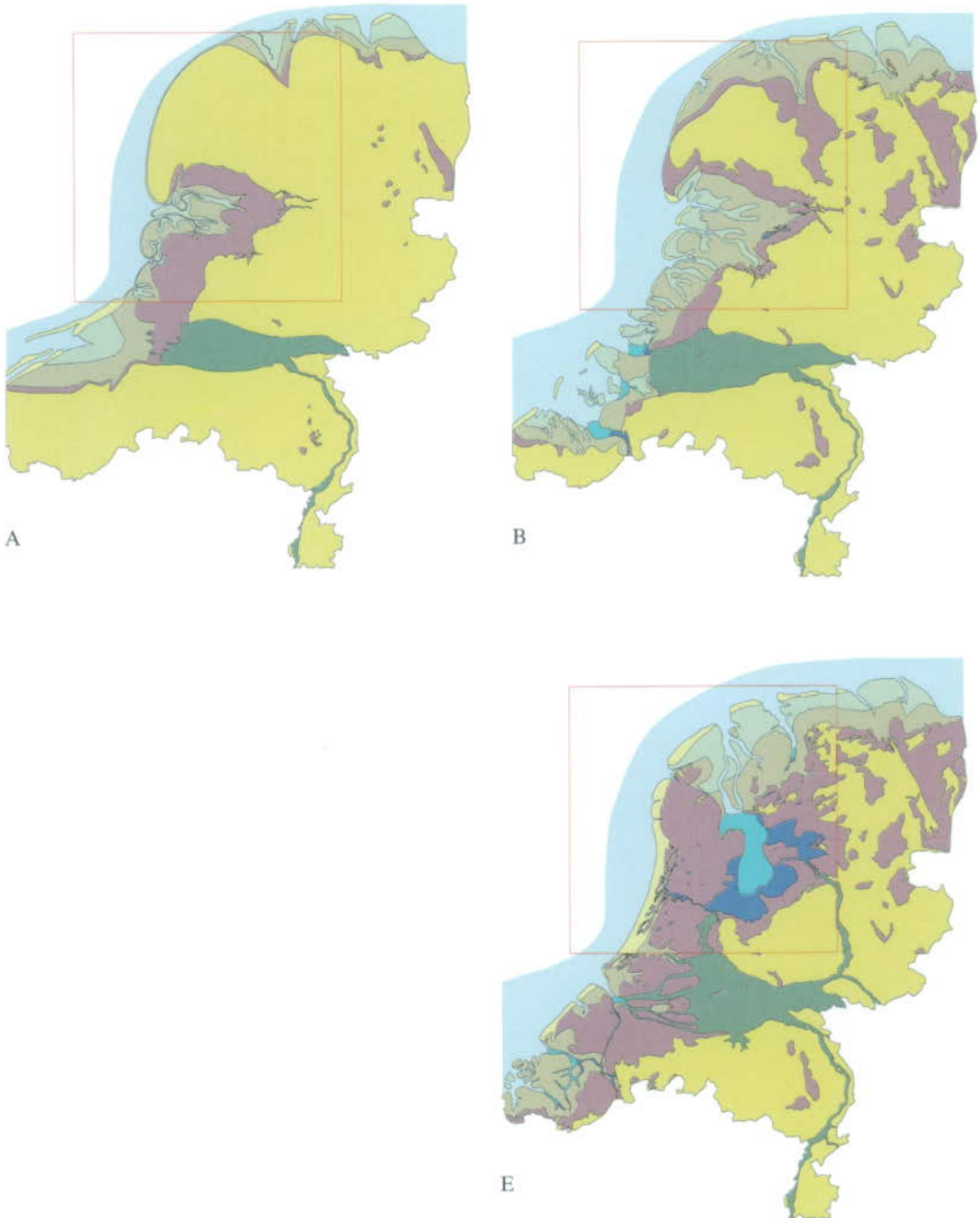
Figure 1. Compiled palaeo-geographical maps of the Netherlands for 6 periods: (A) the Early Atlantic (7000 BP), (B) the Late Atlantic (5500 BP), (C) the Mid Subboreal (3700 BP), (D) the Early Subatlantic (2100 BP), (E) the Early Middle Ages (Mid Subatlantic, 850 AD), (F) the Late Middle Ages (Late Subatlantic, 1350 AD).

C

D

F
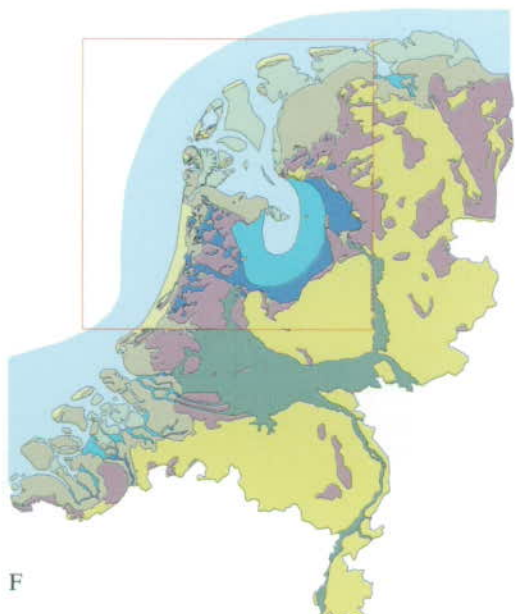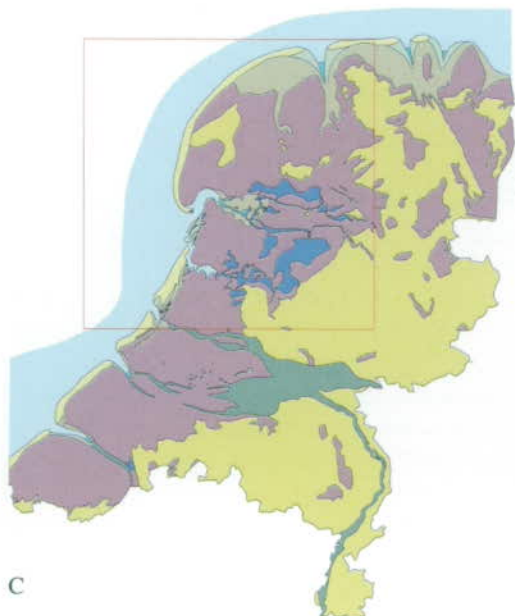
LEGEND

dunes and beachbarriers

salt marshes and mud flats

peat

river deposits

pleistocene areas

salt water

brackish water

fresh water

tidal flats

grazing must have taken place, but there are ample signs that it affected the natural vegetation composition. In general, the environmental impact was very limited (Louwe Kooijmans 1995) and natural conditions prevailed.

4. Enlargement of open water area; first evidence of environmental impact by Man
(3700 BP - 2100 BP)
The virtual closure of the coast line of northern Holland was a turning point in the history of the IJsselmeer area. The freshwater discharge to the west had come to an end. In the former lagoon a further enlargement of the lakes took place at the cost of the surrounding peatlands. Besides, the loss of peatland was stimulated by wind erosion. So-called detritus-gyttja was deposited, a mixture of fine peat particles and fine sand. In this era, a small peat rivulet most probably started to drain the IJsselmeer area to the north.

Especially in the northern part of the Netherlands, saline to brackish conditions prevailed. The influence of the continual sea level rise is visible in the transformation of part of the former peatland area into mudflats and saltmarshes. The total area covered by tidal flats, mudflats and saltmarshes nearly doubled to 10%.

In the riverine area, the sedimentation, due to the rise of the sea level, resulted in an enlargement of the river floodplain. Locally clayey deposits were deposited in previous peatland areas.

Although the palaeo-geographical maps of 3700 BP and 2100 BP do not show many differences, an interesting development had started. From 2500 BP onwards, there is evidence in pollen diagrams for the opening up of the afforested area on the pleistocene surface by Man. Louwe Kooijmans (1995) states that the system of shifting cultivation with plough agriculture and integrated mixed farming resulted in soil degradation and woodlands changing into heathlands (Fig. 2).

The increasing human population also began to exploit the riverine areas. The favourable conditions in this area made a permanent occupation possible. From this time on, cattle grazing greatly affected the character of the landscape by setting back the vegetation succession (see Fig. 2). The dense forests transformed into a more open landscape, a mixture of woodland and grassland. At that time a few thousand people occupied the country and the environmental impact of Man increased. People not only settled in the afforested areas, but eventually also on the saltmarshes in the northern part of the Netherlands (Van Gijn & Waterbolk 1984) and even the margins of peatland were colonised (Van Es *et al.* 1988). However, half of the Netherlands, coinciding with the peatland area in the west and the IJsselmeer area, was still not suitable for settlement and was therefore not affected by Man.

5. Formation of a new lagoon; some recovery of woodlands (2100 BP - 850 AD)
Although the sea level rise had slowed down, sea intrusions increased during the first 800 years of our era. It transformed peatlands into tidal flats and saltmarshes, especially in the south-western part of the Netherlands. In the IJsselmeer area the peatcover vanished because of erosion. The initially small outlet in the north had become broader and acted as an inlet for marine clays. Also salt sea water penetrated in the area at a limited scale, creating a brackish environment.

Human occupation was still largely restricted to the higher pleistocene areas, the riverine area and the saltmarshes in the north. The decrease of the population after the Roman period resulted in a partial recovery of afforested areas (Louwe Kooijmans 1995).

6. Formation of an inland sea; the start of water management (850 AD - 1350 AD)
With the development of tidal gullies in the IJsselmeer area, the tidal influence in the new lagoon increased and started to drain the surrounding peatlands, which made these peatlands suitable for cultivation. So far these peatland areas could still be considered completely natural.
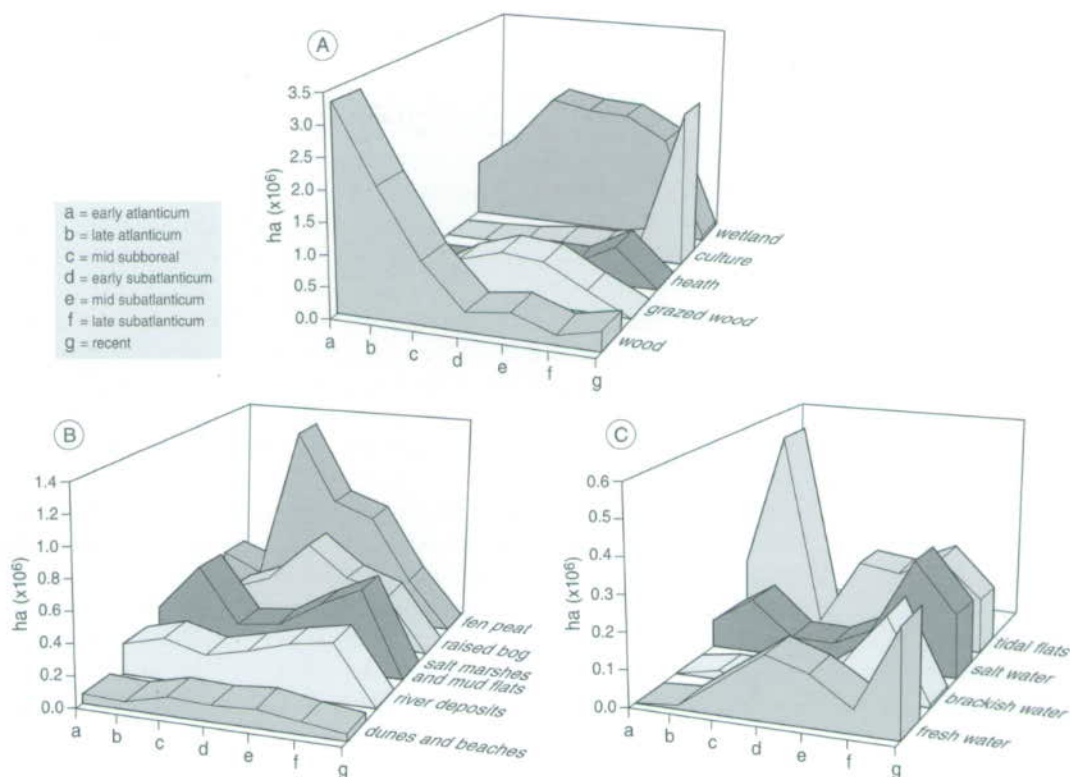
Figure 2. Changes in surface area of main habitat types in the Netherlands for seven periods, including the present situation (see Fig. 1). (A) major terrestrial landscapes, (B) wetland ecotopes, (C) water.

From the eighth century onwards, exploitation of peatland took place which resulted in subsidence and oxidation leading to a drop in the land surface. The human occupation of the peatland areas between Wieringen, West-Friesland and Gaasterland, and Northern Holland made the entire IJsselmeer area more vulnerable to sea influences. Small gullies widened and caused more and more erosion. Large areas of peatland transformed into saltmarshes, tidal flats and shallow open salt to brackish waters. Large-scale freshwater was restricted to the south-eastern part of the IJsselmeer area. Similar processes took place in the south-western part of the Netherlands with the transformation of extensive peatland areas into saltmarshes. The total peatland area was reduced from 24% to 14%.

In the late Middle Ages Man started the battle against the water and tried to protect himself by dikes and dams. In the 12th and 13th century Man constructed dikes not only in the south-western Delta area, the northern saltmarshes and along the Zuiderzee, but also in the riverine area to prevent flooding by river water. This marked the end of free-flowing rivers. Although a large part of the Netherlands was protected by dikes, the situation was by no means under control. Dike breaches and floodings occurred very often and caused a set-back in the situation.

Figure 2 shows the estimated surface area of main landscape types, in a fixed geographical range of the territory now known as the Netherlands. From a diverse, multiple habitat environment it has become a man-made, agriculture-based landscape. Eye-catching for instance is the loss of mesotrophic

fen-peats due to land reclamation and the reduction in surface area of raised bogs due to drainage and cutting.

Clearly the continual speeding up of the actions of Man has greatly altered the extent and composition of Dutch wetlands. Considering the water areas, a tremendous narrowing down of ecologically important transitional zones between water and land has taken place. Around 850 AD some 17% belonged to this category, in 1350 it rose to 33% because of the cultivation of natural areas, declining thereafter to 11% in 1650 and a mere 2% in 1993. Especially the loss of brackish inter-tidal water areas is obvious.

Land use and historical changes in landscape

The period between 1350 and 1600 is characterised by changes caused by the permanent struggle of Man against the water (Van de Ven 1993). The influence of the sea in the IJsselmeer area, the Dollard and in the Delta area caused further loss of land. In the riverine area the river courses were affected by the increasing sea influence. Beside protecting himself by raising the dikes, Man also found ways to reclaim land from the sea.

A new tidal gully between Bergen and Texel together with new reclamations resulted in further loss of peatland and increasing brackish to saline conditions. In 1340 for the first time the term *Sudersee* is used, but it took until 1600 AD for the eastern part of the former Zuiderzee to become saline by a reduced discharge of the river IJssel. By this time the Zuiderzee reached its greatest size. Further deepening of tidal gullies in the Zuiderzee occurred and locally considerable layers of sand were deposited. Deeper inside the basin, clayey sediments with marine shells were deposited.

The human population rose from 750 000 in 1250 to 1 500 000 in 1600. This resulted in the expansion of agriculture, the creation of meadows and a further decline in the area of peatlands. Peat was dredged and dried for fuel on a large scale.

From the 17th century onwards, wind-mills and later on steam engines were used to drain lakes in order to reclaim new land. Figure 3 shows the extent of construction of dikes and polder making from lakes over the last centuries. As time proceeded, ever deeper and larger lakes could be dealt with (Schultz 1992). The damming up of estuaries also caused large changes in the wetland areas. Table 2 shows the embankments and closing off of estuaries which were realised in the 20th century. Also the lowering of the groundwater table caused great changes in the landscape as ever more terrestrial habitat was turned into agricultural land.

Not only did the total surface area of natural habitats decline, also the intensification of land use meant an enormous narrowing down of the variation in landscapes (Fig. 4). It is important to note that, with respect to wetland degradation, the greater part of this development has taken place within a period of no longer than 600 years. With respect to the impact on the vegetation, especially grassland communities were favoured (see Chapter 3, Van Eerden *et al.* 1996). The last 100 years were conclusive with respect to the capacity of Man to govern nature's forces.

A reconstruction of abundance of wetland birds

Prehistoric data

Data of avian finds in prehistoric human settlements in the Netherlands provide information about species composition in different eras. The first finds are available from the period 4000-2000 BC. Clason and Prummel (1979) present data about 33 species of water birds identified in human settlements. Except for the seaducks *Melanitta nigra* and *M. fusca*, the Gadwall *Anas strepera*, the Coot *Fulica atra* and the Purple Heron *Ardea purpurea* which are lacking from this list, virtually all species described are still present in considerable numbers today. The only two species which were present in prehistoric times, but became extinct later on are, according to the finds, a pelican (probably Dalmatian Pelican

850 A.D.

1350 A.D.

1650 A.D.
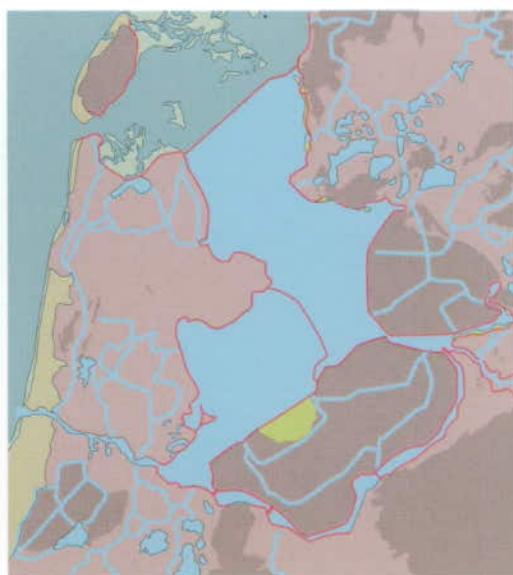
1993 A.D.

WATER	TRANSITIONAL	LAND	
■ natural	■ natural	■ natural	■ intensively cultivated
■ semi-natural	■ semi-natural	■ cultivated	— dike

Figure 3. Human influence on the landscape in the IJsselmeer region by means of the construction of dikes, drainage of lakes and lowering of groundwater tables, for the periods 850 AD, 1350 AD, 1650 AD and at present (1993 AD).

Table 2. Large land reclamations and man-made changes of hydrological regime in water-bodies during the 20th century in the Netherlands. Enclosed water indicated separately.

| Area	Year	Total area (ha)	Remaining water (ha)	Habitat
Carel Coenraadpolder	1927	650		salt-marsh
Wieringermeer[1]	1930	2000		estuary
Zuiderzee	1932	36 5000	365 000	estuary
Linthorst Homanpolder	1941	1300		salt-marsh
Noordoostpolder[1]	1942	48 000		lake
Emmapolder	1945	800		salt-marsh
Quarlespolder	1948	480	50	salt-marsh
Brielse Maas	1949	290		salt-marsh
Braakmanpolder	1952	1550	250	salt-marsh
Dijkwater	1954	170	25	lake
Oost Flevoland[1]	1957	54000		lake
Veerse Meer	1961	4170	2125	sea-arm
Zuidersloe	1963	170		sea-arm
Plaat van Scheelhoek	1965	225		salt-marsh
Zuiderdieppolder	1966	180		sea-arm
Zuid Flevoland[1]	1968	43 000	1000	lake
Lauwerszee	1969	9100	2000	estuary
Haringvliet	1971	9850	7700	estuary
Grevelingen	1971	1390	10 800	sea-arm
Markiezaat	1983	2130	1000	salt-marsh
Volkerak Zoommeer	1987	8250	6250	sea-arm
Oosterschelde[2]	1987	36 900	25 200	sea-arm

[1] polders in the former Zuiderzee area

[2] enclosed by storm-surge barrier with reduced tides
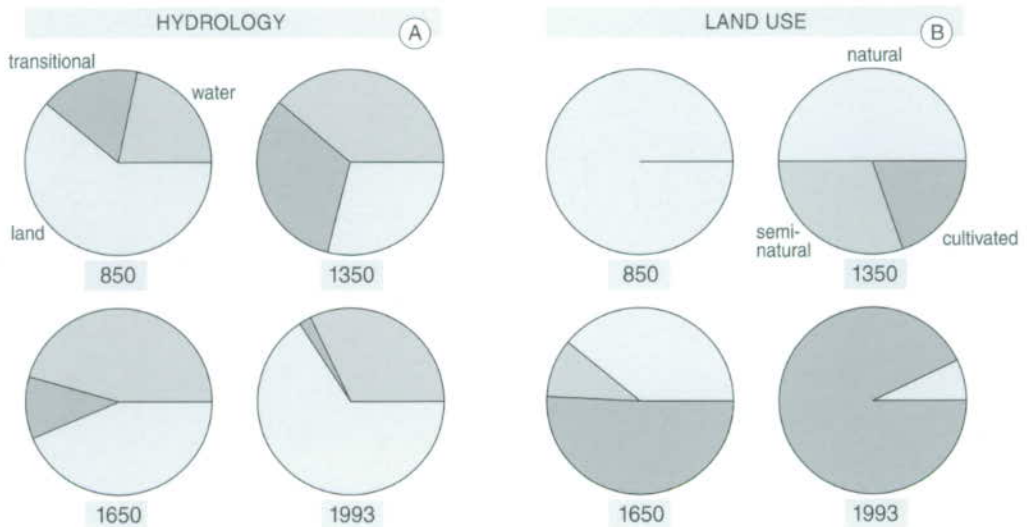
Figure 4. Development of habitat composition in historical time (A) in terms of major landscape types, and (B) scaled by degree of "naturalness" in the same area and for the same time series as depicted in Figure 3.
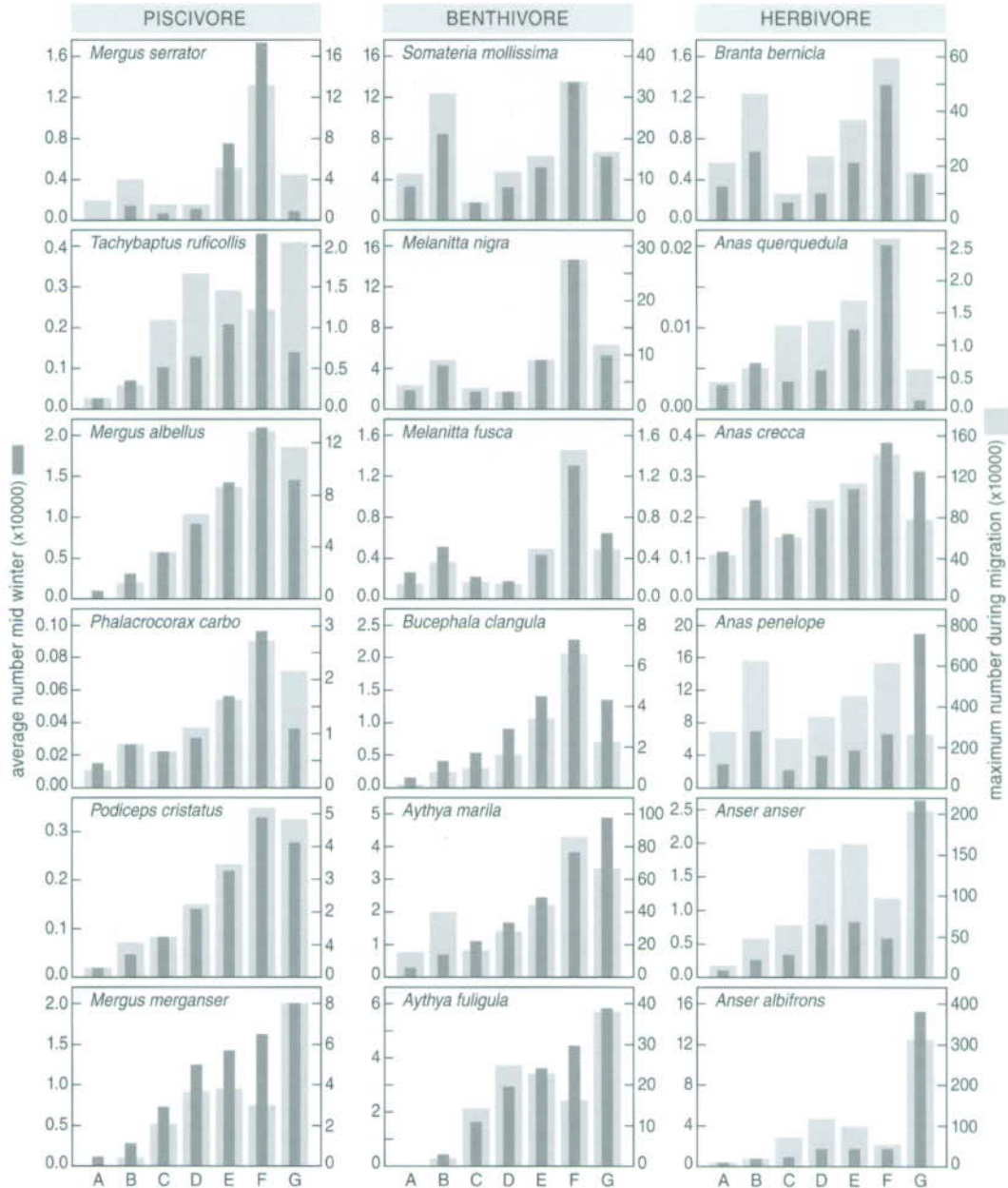
Figure 5. Estimated average population of 18 bird species in the Netherlands, representing three main ecological groups. For periods see Figure 1. Two estimates have been calculated being the peak number during migration and the average mid-winter number which is less, especially in herbivorous water birds. Calculated numbers are considered indicative as peak numbers can only occur if other factors are not limiting.

Pelecanus crispus) and the Great White Egret *Egretta alba*, both species of large-scale fresh and brack-ish water marshes. Also Squacco Heron *Ardeola ralloides* and possibly Little Egret *Egretta garzetta* have become extinct as breeding birds (Vera 1988).

On the basis of the general description of changes in landscape caused by sea level rise and human impact we have attempted to explore the possible effects of these prehistoric habitat shifts on the long-term presence and composition of the water bird assembly. As an example, Figure 5 depicts the esti-mated annual peak and average winter numbers (October-March) for 18 selected species belonging to different ecological groups, showing the most important trends.

In the group of herbivores Brent Goose *Branta bernicla*, Garganey *Anas querquedula*, Teal *Anas crecca* and Wigeon *Anas penelope* have always been abundant. Especially the peak numbers during migration are estimated to have been considerably higher than nowadays, *e.g.* about two to three times around 1350 (Fig. 5). These species feed on saltmarshes, seagrasses *Zostera* spp. in tidal bays and pio-neer vegetations under freshwater conditions. In some species like Wigeon, as well as in Greylag Goose *Anser anser* and White-fronted Goose *Anser albifrons*, numbers during mid-winter have strongly increased in recent times, coinciding with the extension of grassland, which forms their major food source nowadays. Other species, more dependent upon natural food have declined during mid-winter compared to the situation around 1350.

Also benthos-feeding ducks like Eiders *Somateria mollissima*, a marine species, had fluctuating numbers lately peaking during the Late Subatlantic period around 1350. Also Common Scoter *Melanitta nigra*, Velvet Scoter *M. fusca* and Goldeneye *Bucephala clangula* were abundant earlier on with the highest numbers in the period around 1350. A gradual increase over time is apparent in Scaup *Aythya marila* and Tufted Duck *A. fuligula* with the highest numbers in recent years. This trend is based on the great extension of shallow freshwater habitat, which for these species is important habitat as well. Unlike the herbivores, the benthos-feeders do not show large differences between average winter numbers and peak numbers during migration. The trends follow the same pattern for most species.

The third group, that of the fish-eaters generally shows the highest numbers from 850-1350 while in recent times a decline is apparent due to the lower capacity of freshwater as wintering area. This decline is less marked or absent in Great Crested Grebe *Podiceps cristatus* and Goosander *Mergus mer-ganser*. In Red-breasted Merganser *M. serrator* the pattern is comparable to that for the *Melanitta* sea-ducks, being related to the presence of brackish water. High numbers of these species occurred in the period of the Late Subatlantic around 1350.

We estimate that, based on 36 species, the total number of water birds present in winter gradually increased from the Early Atlantic (7000 years BP) until the Late Subatlantic (1350 AD) (Fig. 6). In the latter period several habitat types reached their greatest range: freshwater marshes (390 000 ha), salt-marshes (560 000 ha), mudflats (262 000 ha) and brackish shallow water (111 000 ha), while still con-siderable areas of fen-peats (332 000 ha) and raised bogs (357 000 ha) existed. All categories of water birds peaked in this period, still little influenced by Man (Fig. 6). Thereafter, the extension of grass-lands and arable land was enormous, mainly at the cost of peatland, heather and saltmarshes. This led to an explosive, almost seven-fold increase in the number of wintering herbivorous water birds com-pared to 850-1350 AD, despite the loss of saltmarshes and riverine marshes which form an important habitat for this group. The capacity for migratory herbivorous water birds did not show such a strong increase in recent times (Fig. 6). Concerning the waters, the category shallow open freshwater (<10 m deep, 294 000 ha) which exists nowadays has never been precedented. However, calculated numbers of wintering benthos-eaters (36% reduction) and fish-eaters (45%) have sharply declined, due to the flagrant decrease in brackish and marine shallow waters. Also the planktivorous water birds like Shov-eler *Anas clypeata* are estimated to have declined with some 55% since 1350 AD.

Although the total number of wintering water birds is estimated to be higher today than at any time
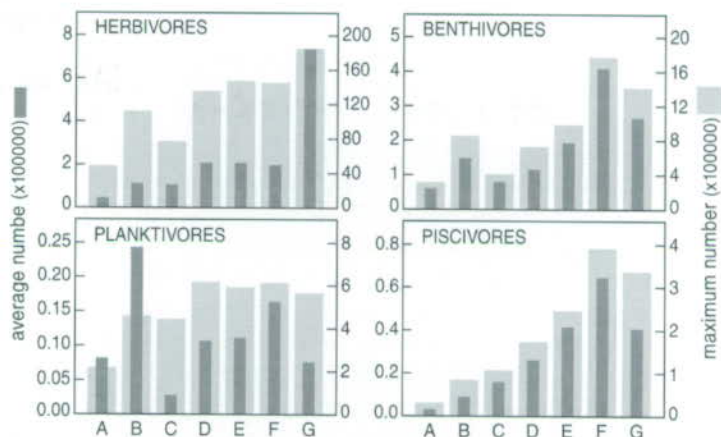
Figure 6. Estimated composition of the avian fauna for seven periods and four different groups of water birds. Calculated total for the Netherlands has been based on peak and average winter numbers cumulative over all habitats. For the meaning of different estimates see Figure 5.

before in the period of study (until 7000 years BP), 17 species of the non-herbivorous water birds have strongly declined during the late Middle Ages due to the land use activities of Man, whilst 15 herbivorous species have increased.

Historical data

Historical data provide especially detailed information about colonial birds, mainly fish-eaters, and the following is illustrative for the role of Man in exploiting and repressing colonially breeding water birds. From sales accounts (1359-1361) it is known that colonial birds such as Grey Herons *Ardea cinerea*, Spoonbills *Platalea leucorodia* and Night Herons *Nycticorax nycticorax* and "White Herons and other white birds" (Van Pelt Lechner 1919 in Brouwer 1954) lived in the Goudsche Bosch, near Gouda. Other sources tell that in 1357 no less than 564 herons and 2000 Night Herons were sold. From the 16th century more historical data are known. Regulations, so-called "Plakkaten", tried to regulate the hunting and catching of birds of importance such as "Perdrysen (*Perdix*), Fesanen (*Phasianus*), Putoren (*Botaurus*), Moerhoenderen (*Tetrao tetrix*), Cranen (*Grus*), Trap-ganzen (*Otis*), Swanen (*Cygnus*), Reijgeren (*Ardea*), Quacken (*Nycticorax*), Schollevaers (*Phalacrocorax*), Lepelaers (*Platalea*) en Berch Eenden (*Tadorna*)", most of which are nowadays important wetland species. Regulations to protect the rights of landowners were also necessary as populations of some species like Swans were known to become exterminated rather easily: "*binnen korten tijdt ... merckelick vergaen ende gedepeupleert is*". In former times the Netherlands harboured internationally well-known important breeding places for birds such as "Het Zevenhuizensche bosch, Schollevaerseiland, Eyerland". All of them, being hot-spots for the species at the time, were successively destroyed by cultivation measures of the landscape or peat-digging. The habitat changed in such a way that it was no longer suitable for colonial birds such as Cormorants *Phalacrocorax carbo*, Spoonbills and herons. "Het Zevenhuizensche Bosch" (near Gouda, about 26 ha) harboured a heronry as early as the 14th century. Around the end of the 17th century the area had been almost completely cultivated "*weggeraeckt en de grond sedert genoegzaem geheel en al weggeveent*". About the fate of the remainder of the colonially breeding birds it is reported that large quantities of young herons, Night Herons, Spoonbills and (most) Cormorants

were shaken out of their breeding trees and were transported by barge to the markets in the cities of Holland : *"seer groote quantiteyt van reygers, quacken, lepelaers... ende meest van alle noch scholle-vaers ... die dan ... uyt haere nesten van de bomen geschudt, ende nedervallende worden alsoo gevan-gen ende met geheele schuyten seffens in alle steden van Hollandt vervoert ende verkoght...."*. In 1668 400-500 young were collected twice a week in this way, some 10 years before this had been about 800. Around 1760 the colonies of these bird species were found once more at "Schollevaerseiland" near Nieuwerkerk (C. Nozeman), where they remained until the second part of the 19th century. Again, numbers were reported as "countless": *"De hoeveelheid van op den naeckten grond aengelegde en bezette nesten, van Scholvers en Reigeren dooreen, was onnoemlyk, en zelfs niet by gissing te begrooten... De Lepelaers, welken ik hier mede broedende vond, maekten verre weg den kleinsten hoop uyt"*. This colony was also heavily exploited and was already greatly diminished in 1864. The birds had moved to lake Horstermeer near Vreeland along the river Vecht. In 1851 there were about 1000 pairs of Cormorants, 700 pairs of Grey and Purple Herons and 1000 pairs of Spoonbills. Egg-culling remained important with maximum numbers collected per week being 800 heron, 1100 Cormorant and 1600 Spoonbill eggs (Brouwer 1954). In 1865 this breeding colony was almost completely extermi-nated and the lake was subsequently reclaimed in 1883 (620 ha).

We may conclude that with respect to the species composition, the avian fauna of wetlands in the Netherlands has not changed dramatically in the last 7000 years. However, the exploitation of birds used to be common practice and this had a reinforcing effect upon habitat loss from the 17th century on, especially on the disappearance of many breeding colonies of fish-eating birds.

Discussion

From a natural towards a Man-made delta
The enormous impact of Man on the continually changing outlook of the Netherlands has been empha-sised. Especially the short period of time during which these changes occurred was unequalled in the past. Many land reclamation projects were realised, most of them not or only marginally documented with respect to their biological significance.

As an example we will briefly discuss the Zuiderzee project in this context. The construction of the Barrier Dam (1932) heralded a new period of dominance of freshwater lakes. Within 5 years the brack-ish Zuiderzee changed into the largest freshwater lake in western Europe with a surface area of 3650 km^2 (lake IJsselmeer). Beside a reduced risk of floods, the length of the coastline had been shortened to improve the water control in and outside the IJsselmeer area. Later on, reclamation of parts of the lake bottom resulted in a major decline of the lake area in favour of a considerable enlargement of the agricultural area. Successively, the Noordoostpolder (1942), Oostelijk Flevoland (1957) and Zuidelijk Flevoland (1968) were constructed; a total of 1650 km^2. Further compartmentalisation of the lake was caused by the dike Enkhuizen-Lelystad (1976).

What was the effect on the natural values in the area? The sudden transition of an open, gradient-rich water system into a closed, more uniform water body brought about the greatest changes for the plankton, benthos, fish and mammal communities (De Beaufort 1954). For example, before the closure 52 species of fish were known to inhabit the area, some of which were anadromous migrants (Havinga 1954). In the IJsselmeer the species composition was greatly reduced as 26 species became extinct (Fig. 7). The extinction of local races of Anchovy *Engraulis encrasicholus* and Herring *Clupea haren-gus* was not only a dramatic biological event but also negatively affected the position of the local fish-ermen. Also mammals such as Harbour Porpoises *Phocoena phocoena* and Common Seals *Phoca vitulina* disappeared completely. Although the bird community changed in numbers, no major loss of
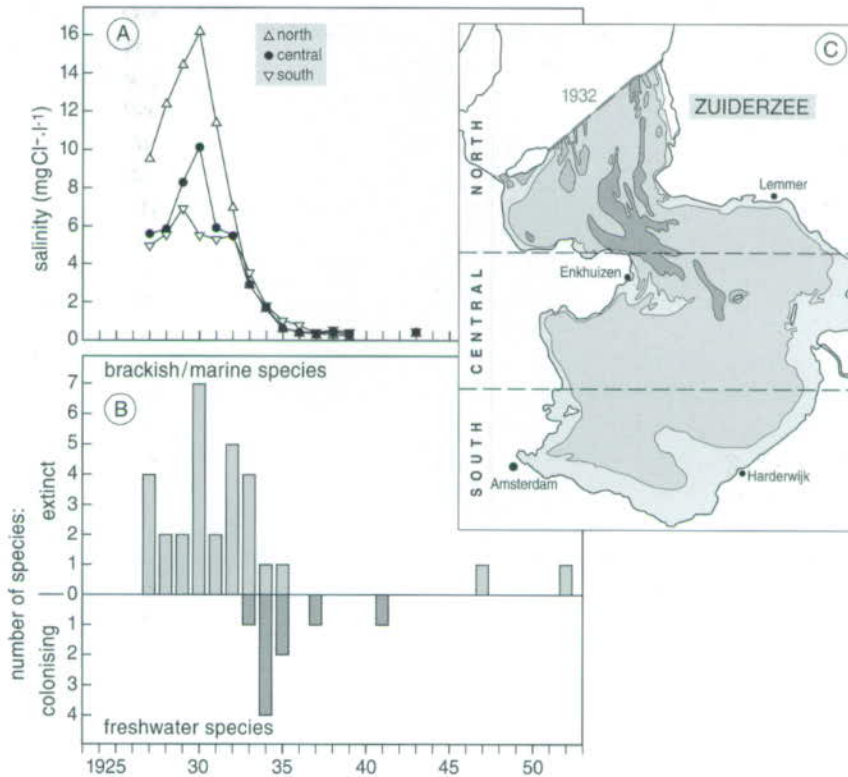
Figure 7. The effect of closing off the Zuiderzee on salt content at three sites in the area (notice gradient!) and the recordings of either extinction or major expansion of fish species. Data compiled after Havinga (1954). Contrasting to birds, system-bound species like fish incurred severe losses at the level of species occurrence.

species occurred. On the other hand, many of the remaining freshwater fish and benthic species could expand enormously. For instance, newly established populations of Zebra Mussels *Dreissena polymorpha* since 1934 have expanded greatly in the lake (Van Benthem Jutting 1954), as did the salmonid Smelt *Osmerus eperlanus* (Havinga 1954). The latter managed to increase spectacularly in biomass and to shorten its life cycle; from an anadromous spawner in its third season, Smelt became mature within one year as non-migrants in the stagnant freshwater situation. Both *Dreissena* and *Osmerus* play a very important role *e.g.* as food organisms in the system nowadays (see Chapters 13-19). The human fisheries shifted target and now concentrate on the freshwater species Eel *Anguilla anguilla,* Perch *Perca fluviatilis* and Pikeperch *Stizostedion lucioperca* (Buijse 1992, Buijse *et al.* 1993, Dekker 1997).

We consider the example of the transformation of the Zuiderzee into the freshwater lake IJsselmeer and the subsequent large-scale land reclamation illustrative for the recent changes that have occurred in many Dutch water systems. It shows how specialist organisms which depend tightly on a particular type of landscape react very sharply. This will also have been the case in natural changes as, for example, from fresh to marine conditions and from oligotrophic fen-peats to estuarine clay marshes as happened many times in prehistory. Many of the effects on species of invertebrates and fishes that were involved remain unknown and undoubtedly this is also true for many species of mammals, amphibians,

(A) Mosaic of Reed *Phragmites australis* and Marsh Fleawort *Senecio congestus*, formed by differences in water table and selective grazing by herbivorous water bird. (B) Close-up, Oostvaardersplassen, June 1988.

insects, higher plants, mosses and lichens. Birds, which are less strictly confined to one system (they operate on a mega-scale because they can fly), can respond with a change in numbers over a much vaster area. Although this change can be dramatic, a complete extinction is rare. If a suitable habitat reappears, however, birds may colonise these areas again. This happened with the nature development project in the Oostvaardersplassen where in 1978 Great White Egrets recolonised the Netherlands as a breeding bird after a period of absence of *c*. 600 years (Poorter 1980).

During this century also the within-habitat degradation has levied its toll. The examples of water pollution (eutrophication, contamination), disturbance by fishing, hunting and recreation as well as the deteriorating effects of habitat shrinkage are well-described, and a general policy to counteract these effects has been approved (Ministry of Transport, Public Works and Water Management 1989, Ministry of Agriculture, Nature Management and Fisheries 1990). Less known are the effects of the levelling down of oscillation of natural processes which cause a set-back of succession (*e.g.* erosion, sedimentation, water level fluctuation and fire). Proposals to eliminate or reduce these effects are now being discussed (Rhine-Meuse delta: Smit *et al.* 1994, large lakes in IJsselmeer area: Iedema 1996, larger freshwater marshes (Oostvaardersplassen): Van Eerden *et al.* 1995).

Long-term effects upon carrying capacity for wetland birds

Because they can fly, birds are able to reach isolated patches of wetland. Compared to mammals and some plant and insect groups, birds respond faster to changes in habitat availability. Due to this highly versatile behaviour, only three species of water birds have become (locally) extinct in the last 7000 years according to archaeological finds: (Dalmatian) Pelican, and/or historical data: Great White Egret (14th century, Vera 1988) and Squacco Heron (*c.* 1860, Vera 1988). Many other populations of herons have become extremely scarce such as Night Heron *Nycticorax nycticorax*, Little Bittern *Ixobrychus minutus* and White Stork *Ciconia ciconia* or they have an unfavourable status (Bittern *Botaurus stellaris*). This group of breeding birds, amplified by Garganey *Anas querquedula*, has both the loss of feeding territory in the Netherlands as well as a deteriorating wintering situation in Africa (drought, drainage and transformation of wetlands) in common. Most of the anatid water birds, however, still have their breeding grounds intact in the remote areas of Iceland, Scandinavia and Russia. Although their wintering area has greatly changed, no species seems to have become (locally) extinct yet. However, as we showed, their population size must have changed considerably.

By his tremendous impact on the landscape, Man has had an enormous effect on the carrying capacity for water birds. Not only in the Netherlands, but also along the coasts of the Baltic many archaeological finds of water birds are known from early settlements of Man. For example, in Sweden Cormorants have extensively bred in ancient times and the oldest records date back to 9000 BP (Ericson & Hernández Carrasquilla 1997). After severe persecution the species became extinct here as a breeding bird in 1909. In Denmark Dalmatian Pelican was described as breeding in the period 6000-4000 BP (Løppenthin 1967). Spoonbills were considered to have colonised Denmark first in the 14th century. A severe storm in 1362 had been the cause of many new wetland areas which were formerly not available. Later on, like in the Netherlands, cultivation measures caused the disappearance of many wetlands, and Spoonbills and Cormorants became completely extinct in this country during the 20th century (Gregersen 1982).

The most important effects of Man's actions include (1) habitat loss by the transformation of nature into grassland and arable land (with a reduced flux in groundwater levels), (2) a reduction in surface area of shallow brackish and marine waters and (3) banning the effect of the tides by construction of large infrastructural works, which causes the disappearance of transitional zones. The avian fauna of the group of water birds has shifted from a pluriform assembly to one dominated by herbivorous birds. The carrying capacity for fish-eaters (45% less), benthos-eaters (36% less) and plankton-eaters (55%

less) has declined enormously. The only natural large-scale habitat still present is that of the Wadden Sea. As a sign of remnant of past glory, this area is subject of much concern in relation to questions about nature management and the desirability of joint use, putting this area under greater pressure. This concern is justified given the relatively small change in surface area of this habitat over the different periods (Fig. 2).

How reliable are the calculations of our reconstruction? Data about bird density per habitat type necessarily come from recent investigations. We can, however, not completely oversee all effects of landscape diversity and species composition on bird use. Also the availability of aquatic communities of the past may have been different from the situation we know today. Moreover, the effect of scale on total numbers can only provisionally be extrapolated from our present-day experience. The historic densities may therefore have differed from the actual ones. A clear example of our incomplete knowledge is the effect of eutrophication which could not be taken into account. It is well-known that water birds respond to enriched food situations (*e.g.* herbivores see Chapter 3, Van Eerden *et al.* 1996; benthos-eaters Chapter 14; fish-eaters Van Eerden *et al.* 1995). By using recent data for extrapolation into the past, this effect will lead to over-estimation of bird abundance in ancient times. On the other hand, food availability may have been greater because of unknown resources and the previously mentioned effect of scale of habitat. The conclusion from this is that the effects described before can either have been greater or smaller. The data are therefore to be considered with caution, but, as we see it, they do show the likely trends. The prehistoric phase was by no means more rich in numbers of water birds than today, at least not in winter. This is largely due to the estimated small number of herbivorous water birds that can be taken up during midwinter in areas as fen-peats, wet heather and the afforested parts which have dominated the landscape for a long time. Only on passage in autumn and spring do these areas provide more food, and this may have attracted more birds on passage, given the presence of enough winter habitat elsewhere. Because we know little of the primeval situation further to the south (*e.g.* the British Isles, the French west coast and the Iberian Peninsula) as a winter habitat, the comparison of our estimated peak and mid-winter numbers remains tentative. However, at least in the case of the herbivores the effect of shortstopping, that is shortening the migratory flyway and wintering further north, is suggested by Figure 6.

Evaluation of the occurrence and functioning of Dutch wetlands

At present, natural landscapes contribute no more than 30% of the total surface of the Dutch territory (excluding deeper coastal sea water). Most of this consists of water, tidal flats and coastal habitats (salt-marshes, dunes). Maybe as a consequence of the long-lasting transformation of wetlands into agricultural land, the public consciousness about nature and natural values rose steadily. Hunting legislation, the creation of "nature reserves" since 1905 and educational programmes have been important steps to preserve the remaining natural values. So much was lost recently that even studies abroad in so-called reference areas (relatively undisturbed areas, comparable to the Dutch situation in the past) were undertaken, in order to find out what should be aimed at. Even now, the question as to what extent bird numbers are regulated by available food stocks in natural and man-made habitats remains largely unanswered. This is the more oppressing as questions about the effect of large-scale habitat changes are still going on (*cf.* discussions about the effects of a second national airport, the sea-ward extension of industrial areas and the continual urbanisation in the Netherlands).

Effects of habitat deterioration caused by acid rain, fragmentation and disturbance are beyond the scope of this paper. What has been elucidated here is the dramatic turnover of habitats by the increasing banning of natural dynamic processes. Sedimentation, erosion, the changing coastlines and course of rivers and streams as well as the gradient situations brought about by tidal forces are largely diminished. As a consequence of closing off the sea-arms the polluted sediments affected the food chain in

the newly created water bodies (*e.g.* Bijlsma & Kuipers 1989). Active management as to replace these natural processes by mowing, cutting and grazing (Bakker 1989) preceded measures like the reintroduction of species and proposals about the rehabilitation of natural processes by the restoration of the former super-abundant connections between rivers and the sea (*e.g.* Smit *et al.* 1994).

Early successional stages in wetlands have become extremely scarce. The importance of this originally super-abundant facet (see Fig. 1) is one of the missing links in our thinking about the functioning and maintenance of present-day wetlands. This point will be emphasised elsewhere (*e.g.* Chapter 8). As to the newly created land areas, the embankments are often followed by a pioneer stage of marshland and/or extensive agriculture. This phase is attractive to many bird species as it is a highly productive period (seeds, insects, young fish and small mammals *cf.* Dijkstra *et al.* 1995, Dijkstra & Zijlstra 1997). By a continual process of developing new areas by draining of wetlands, the loss of wetlands was flanked by the occurrence of Man-induced pioneer phases at the transition of water and land during a period of several hundreds of years. This has unintentionally toned down the effects of loss of area and will have had a temporary, positive effect on those species groups which use multiple habitats, such as water birds. Especially now, when these pioneer effects have faded out and the last large-scale waterworks have been carried out, we are at the onset of a new phase in history. Before we can judge this effect we have to consider the present functioning of natural and Man-made wetlands in more detail.

The present biological significance of Dutch wetlands may seem of modest interest if compared to the situation of the past. Many nature reserves preserve fragments of habitat that was much more extensive earlier on. Many of them have a regulated water level and strongly depend on Man's management of the landscape. A great many have even been derived from cultivation measures (*e.g.* peat cutting activities) and there is a general lack of transitionary zones. However, on an international scale, the Dutch environment still functions as a major haunt for millions of migratory water birds (*cf.* Wolff 1988). Many birds still profit from the remaining wetlands and agricultural areas on their bi-annual journey to and from the breeding grounds. It is this international responsibility to preserve these populations on a mega scale, being the flyway of the species, that makes the effort for an adequate wetland management worthwhile. The question of the "restoration of naturalness" (a hot topic in Dutch nature conservation) should be considered also in relation to this goal. Any endeavour towards a more natural situation, based on a reference from the past, could easily lead to a deterioration of the carrying capacity for migratory water birds. This group of organisms, which has been able to withstand changes over a long period of time, still depends for part of the year on purely natural and unspoiled ecosystems in northern Europe. Only by preservation of their stopover and wintering habitats, necessary as stepping stones along the flyway, their role in these ecosystems can be safeguarded. As the wintering areas have diminished so strongly in size, this requires a fair knowledge of the carrying capacity of these habitats.

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Chapter 3

The response of *Anatidae* to changes in agricultural practice: long-term shifts in the carrying capacity of wintering waterfowl

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The response of *Anatidae* to changes in agricultural practice: long-term shifts in the carrying capacity of wintering waterfowl

Herbivorous waterfowl have greatly benefited from changes in agricultural practice. Winter feeding habitat improved by the intensification of agriculture. The response by *Anatidae* in the Netherlands was that 11 out of 17 herbivorous species have increased. The effects first became apparent for the larger species (1950s-1960s), whilst the highly selective smaller species have responded recently (1970s-1980s). Particularly the improved quality of grasslands (crude protein, increased digestibility, longer season) has resulted in a higher carrying capacity for the true grazers among the avian herbivores. In some species, this is merely a reallocation of numbers along the flyway (Wigeon *Anas penelope*), as in others it is a reflection of the increase of the population as a whole (Greylag Goose *Anser anser*). It is argued that in the near future a reduction in the nitrogen fertiliser application, the loss of grassland in favour of maize silage production and the reduction in the number of cattle which no longer graze in natural areas may lead to a reversed trend. Especially the smaller species such as Wigeon and Brent Goose (*Branta bernicla*), but, depending on the extent of the decline in food quality, also the larger species are likely to be affected, and at the current high population density these species may redistribute themselves over other areas and will locally attempt to exploit other sources of high quality food such as winter cereals. Since the remaining intensively used grasslands as well as the winter cereals will attract higher numbers of waterfowl, an increased conflict with human interests may arise in the future.

Introduction

Few populations of wild animals have been monitored so long and over such a large number as the ducks, geese and swans (*Anatidae*) have. Frequenting wetlands, coastal shallow waters as well as agricultural habitats, this group of species occurs in a wide variety of biotopes. Due to the fact that, in winter, their northerly breeding areas become unfit to live in because of climatic conditions, these birds then form greater concentrations compared to the situation in summer. Because of this habit, country and continent wide surveys have been carried out during the past decades, which have resulted in fair population estimates and a good knowledge about trends in numbers in Europe (Monval & Pirot 1989, Rose & Scott 1994). Few attempts have been made so far to relate changes in numbers and distribution to quantitative ecological causes. The amount of rainfall in the Sahel zone in Africa affects the winter survival in a number of waterbirds *e.g.* in Purple Heron (*Ardea purpurea*) (Den Held 1981, Cavé 1983). On the breeding end of the flyway, much discussion has been going on about the role of Lemming (*Lemnus lemnus*) cycles affecting egg and gosling survival in arctic breeding geese by annual changes in predation rate by foxes (Summers 1986, Ebbinge 1989). Many geese being quarry species, the effect of changes in hunting practice was considered of major importance to the increase in the populations of White-fronted Geese (*Anser albifrons*) and Brent Geese (Ebbinge 1991). Mooij (1991) demon-

strated the tremendous effect of redistribution and increase in numbers of *Anser* geese after the establishment of protected areas in the Lower Rhine area in Germany in 1975. Although mentioned by many authors, changes in agricultural practice have never been analysed in detail to show their possible contribution to changes in waterfowl abundance. The dependence of waterfowl on high quality food has been observed for quite a while (Owen 1971, 1973). This paper aims to describe the tight relationship between herbivorous waterfowl and agriculture. Following a historical overview, the past three decades have been used to describe the changes in land use in combination with the response by the different species of *Anatidae*. Both habitat shifts and numerical response were recorded for this purpose. We focus our study on the Netherlands which, within Western Europe, is the country where the most advanced intensification measures are taken.

Changes in agriculture

Changes in land use
Some 7000 years ago the shift in climate from the *Atlanticum* into the *Subboreal* coincided with an important cultural shift by the then living inhabitants of Western Europe. From a hunting and fishing community, the start of a farming culture was evident (Van Zeist 1959). Clearing of the original forests by the "slash and burn" technique resulted in open patches which were used for the cultivation of primitive crops for several years in succession. Although pigs were used by these traditional tribes, it was not until 5000 years ago that husbandry with the use of barns became common practice. Larger farms started only to occur after around 2000 BC, when horses became domesticated and land use could therefore further expand. However, still much of the forests remained. Systematic fields are recorded 2500 years ago and fertilisation with humic substances was practised (Brongers & Woltering 1978). From Roman times on hayfields were in cultivation in Western Europe, and during this period cattle grazing on the saltmarshes around the North Sea caused an expansion of the grassland vegetation.

Land use intensified greatly after 1000-1200 AD During this period, and again after 1400 AD, a large clear-cut of the original forests was carried out. The construction of the first dikes also occurred in this period, which meant another expansion of the area used for agriculture. The use of wind (windmills, 16th century) and later also coal (steam engines, 18th century) allowed for the drainage of marshes and the reclamation of the ever larger and deeper lakes in the lower parts of the Netherlands (Schultz 1992). The latest territories gained from nature this century were created by the reclamation of the former Zuyder Zee. Here, between 1928 and 1968, *c.* 185 000 hectares of extensive arable and pasture land were created. With the aid of artificial fertiliser, large areas of heathland and moors on sandy soils were also turned into productive fields (Anonymus 1990). This process of a continual progress towards the margins of what is achievable from an agro-economic point of view, led to the situation that, today in Western Europe, 60% of the total land surface is in use for farming. From 1900 till 1990 the area in use as permanent grassland in the Netherlands has varied between 1.1 and 1.4 million hectares. Another 1.4 million hectares are in use for horticulture, greenhouse culture and arable farming (Landbouw Economisch Instituut & Centraal Bureau voor de Statistiek 1960-1993).

Fertiliser application
Beside the increased area in use for agriculture, the application of fertiliser (N, P, K and Ca) caused an increase in the yield of both grassland and arable crops. Applied sporadically before 1900, this became common practice after World War II. As in most ecosystems, nitrogen plays a key role in the determination of the level of plant growth. The addition of this element is fundamental in today's farmland management (Lewis 1986). Most nitrogen is applied in the form of calcium-ammonium nitrate.

Figure 1A shows a sixfold increase in kg N ha^{-1} year^{-1}, applied on permanent grassland in the western part of the Netherlands (1939-1992). From 1981-1990 the amount of fertiliser is highest with on average *c.* 300 kg N ha^{-1} year^{-1}, after which a decrease occurs due to governmental regulations, aiming at the reduction of the total livestock. As is shown in Figure 1B, the yield, expressed in terms of net available energy for lactating ruminants (kVEM ha^{-1} year^{-1}), increased gradually but much slower over the same period, from 7300 to almost 9000, *i.e.* one fifth of the increment of nitrogen application. In the arable sector, the use of fertiliser in combination with better drainage and selection of high yielding cultivars, also resulted in an ever increasing annual production (Fig. 1C, D). Especially for wheat and potato crops this more than twofold increase is remarkable (1948-1989).

A side effect of the increased production of fertilised grassland is the extension of the growing season. The effect of nitrogen fertiliser upon the advance in the date of first cut in spring is 10-30 days, being most obvious on wet peat soils (Van Steenbergen 1977). Due to the presence of surplus nitrogen in the bottom, grass can presently grow for a longer period during late autumn. A higher protein content in the leaves of wheat gives a higher photosynthetic activity (Groot 1989). However, although not combined in growing trials, Sibma and Alberda (1976) showed a lower response of grass leaves to the same intensity of light in autumn than in spring. This means that prolonged growth will occur in late autumn only at extreme nitrogen conditions in the soil (200-400 kg N ha^{-1} year^{-1}, depending on soiltype), under mild weather conditions (temperatures > 2 °C).
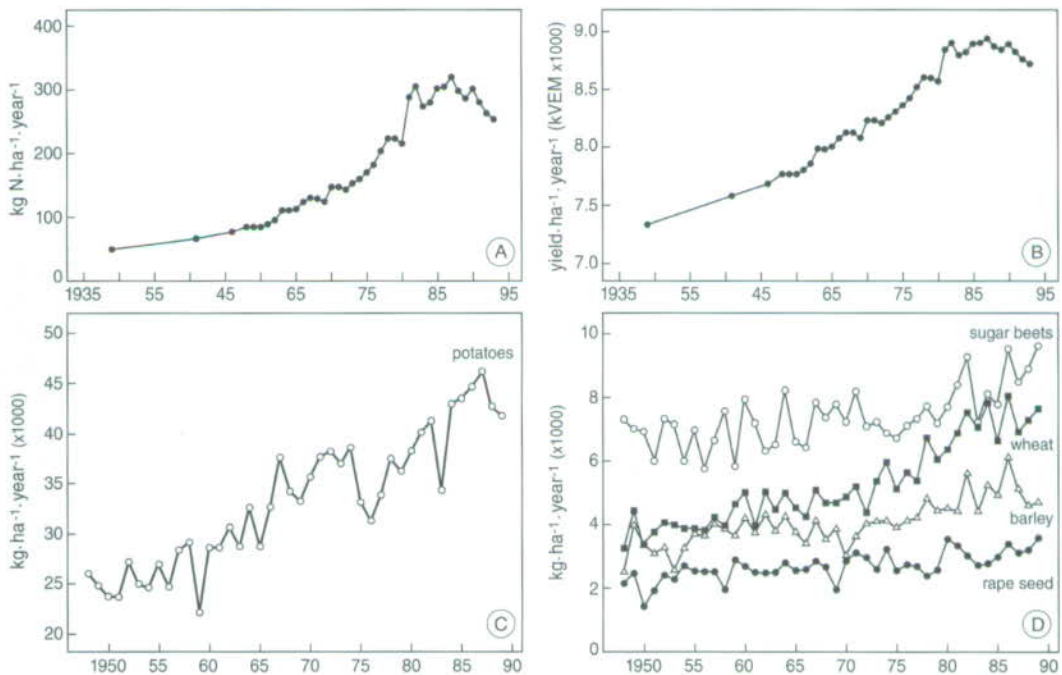
Figure 1. (A) Average annual nitrogen application to grassland in the Netherlands. Data refer to the low grasslands on peaty soils. (B) Changes in yield of grass, expressed as feeding units for lactating ruminants (VEM) thus combining biomass and food quality. (C) Changes in yield of potatoes in the Netherlands. (D) Changes in yield of cereal crops and sugar beets in the Netherlands. All data from Landbouw Economisch Instituut & Centraal Bureau voor Statistiek (Agricultural Economics Research Institute & Netherlands Central Bureau of Statistics).
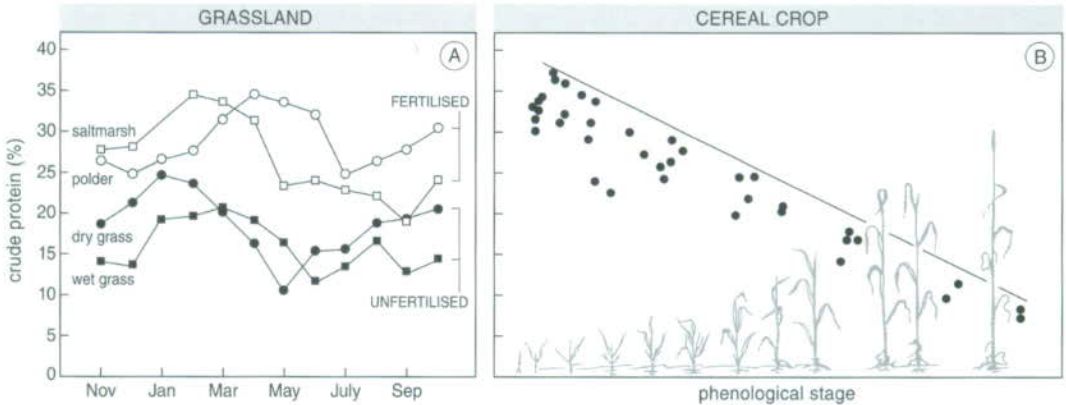
Figure 2. (A) Monthly variation in crude protein content in green leaves of grasses on fertilised farmland and high saltmarsh on the Wadden Sea island Schiermonnikoog and unfertilised drained and wet grassland in the Oostvaardersplassen, Flevoland. All differences between fertilisation levels significant (Sign tests $P < 0.01$). (B) Crude protein content of leaves of winter wheat in relation to plant age. Line shows physiologically achievable maximum. Data redrawn from Groot (1989). Notice the superior position of the quality of young cereals compared to grass (Nov.-Feb.).

Other changes in management

The continual search for high yielding grasslands led to a predominance in the sward of cultivars of *Lolium perenne*. At the Dutch Nitrogen pilot farms, which were monitored from 1949-1991, the percentage of *Lolium* in the sward increased from 24 in 1950 to 71 in 1990. However, on the moist peaty soils no more than 50% consisted of this species (Keuning 1994). The total number of species decreased from 30 to 19 over the same period (Keuning 1994). Reseeding and renovation of the entire sward (up to 150 000 ha year^{-1}) are the main causes for this predominance. This practice started to increase soon after 1970 as a result of the intensification of dairy farm management (Sibma & Ennik 1988). Increased damage of the sward may occur as a result of a high number of cattle (trampling, scorch), slurry application by heavy machinery in winter and increased vulnerability for frost. Another effect of the increasing herds of cattle was the need for more grazing areas. The farmers improved the quality of previously marginal areas in terms of economy by nitrogen application, hay-making and the introduction of livestock in these areas. In the Dutch part of the Wadden Sea area for example, this has led to the intensification of the use of saltmarshes in the Ems/Dollart area, on the islands of Schiermonnikoog and Terschelling and along the coast of Friesland. The period 1970-1985 formed the peak in this process after which governmental legislation led to a reduction in the number of cattle, which in turn lessened the use of saltmarshes by farmers (Bakker 1989, Dijkema 1991). Figure 2A shows year-round monthly changes in content of crude protein in grass leaves for a fertilised polder and a high saltmarsh at Schiermonnikoog, in contrast with unfertilised wet and dry grassland in the Oostvaardersplassen. The natural vegetation of the higher saltmarsh (*Festuca rubra*) and the unfertilised swards (*Lolium perenne*, dry, *Agrostis stolonifera*, *Alopecurus geniculatus*, wet) had an annual peak in crude protein content between January and March, whereas the heavily fertilised polder had peak values later, between April and June. The difference between fertilised and unfertilised swards is highly significant (Sign tests $P < 0.01$), but within each group no significant differences existed.

In the arable sector the mechanical harvest of root crops, which started already before the turn of this century, meant a sharp increase in the presence of spilled biomass to which the continual increase

in crop yield can be added (Fig. 1C, D). The introduction of highly palatable Rapeseed *Brassica* without Eruca acid during the 1980s further improved the feeding conditions of herbivore birds (grey geese *Anser* and Whooper Swans *Cygnus cygnus*) and mammals (Roe Deer *Capreolus capreolus*) in winter. Figure 2B shows crude protein content of leaves of winter wheat in relation to the age of the plants. Compared to grass, the high quality of young leaves of cereals is evident as well as the continual decline with proceeding age, typical for all graminoids in non-grazed situations.

There are two management measures that have clearly led to a less potential food supply for waterfowl. First, due to better sowing machinery, the plant density in cereal fields has decreased remarkably over the past decades, which meant a reduction in potential leaf biomass available during winter. Also the period of sowing of cereals was delayed from September/early October to November which has also resulted in a lowered standing crop in winter. Second, the high yielding strains of *Lolium* are sensitive to frost which may cause a rapid deterioration of the sward. Also late autumn application of fertiliser, late mowing in November and the use of slurry in winter stimulate the growth of grass during winter which increases the risk of frost damage (Keuning *et al.* 1988). The latter effect is, however, to a large extent compensated for by the availability of recently reseeded fields which are less sensitive (Huokuna & Hiivola 1974).

Responses of *Anatidae*

Early response of *Anatidae*

First some 2500 years ago, wild *Anatidae* may have experienced the first effects of agricultural practice in Western Europe. The cultivation of cereals meant the presence of stubble in autumn of which species such as Mallard *Anas platyrhynchos* and Greylag Goose *Anser anser* could have taken advantage locally. Finds of these species and the early domestication of the two suggest an early affiliation with Man. In the Roman period the presence of hayfields may have attracted the first true grazers, but the extensive marshes probably provided food for most waterfowl then (Owen 1980). The habit of feeding on cereals and pastures by wintering *Anatidae* probably originates from the period 1400-1600 AD, when farming on a larger scale became the rule. However, details about numbers and species involved are not available. Kear (1963a) describes the more recent habit of potato-eating by waterfowl in Britain. After its introduction in 1590, potatoes have been commonly grown since 1750. Only after two hard winters and the occurrence of potato blight, Mallard was the first species recorded to take profit of this new food supply (1863). Somewhat later, in Scotland around 1890, Pink-footed Geese *Anser brachyrhynchus* turned to this food for the first time. By the 1920s this habit was widely spread among the wintering populations of these two species in Britain. Greylag Geese have followed much later, since 1935, whereas White-fronted Geese and Barnacle Geese *Branta leucopsis* have never been observed to take part in this habit so far (Kear 1963a, Owen 1980). Thus once established, the tradition of feeding on a certain food is maintained in the population. Different species or populations have reacted at different times. Greylag Geese in the Netherlands, for instance, shifted to potatoes much later, around 1955 (T. Lebret pers. comm.) and this food source is of no importance to continental populations of Pink-footed Geese.

Response during the 20th century

Recent changes in agricultural practice have had a tremendous impact on waterfowl populations after World War II. Most herbivores are directly affected by changes in food supply, other groups are indirectly affected through changes in water quality. High nutrient loads in freshwater ecosystems have led to a switch from a clear water/macrophyte dominated system to a turbid water/algae dominated system

Table 1. Habitat use by different species of *Anatidae* in the western Palaearctic which partly depend upon agricultural habitat in their annual cycle. Time in habitat estimated in months *per annum*, weighted for the entire population based on the relation with feeding. Species have been listed in order of decreasing importance concerning the use of agricultural habitat (arable and pasture).

b breeding, s during summer, a aquatic feeding.

Species	arable w. Eur.	pasture w. Eur.	nature w. Eur.	total w. Eur	nature or elsewhere
Cygnus olor Mute Swan	1	8 b,a	3 a	12	0
Anser fabalis Bean Goose	7	2	0	9	3
Anser anser Greylag Goose	6	3	3 a	12	0
Cygnus cygnus Whooper Swan	5	3	2 a	10	2
Anser albifrons White-fronted Goose	3	5	1	9	3
Cygnus columbianus bewickii Bewick's Swan	2	5	2 a	9	3
Anser brachyrhynchus Pinkfooted Goose	3	4	1	8	4
Anas platyrhynchos Mallard	4	3 b,a	5 a	12	0
Branta leucopsis Barnacle Goose	1	5	2	8	4
Branta bernicla Brent Goose	+	5	4	9	3
Anas penelope Wigeon	0	5	2	7	5
Anas strepera Gadwall	0	4 b,a	5 a	9	3
Anas clypeata Shoveler	0	4 b,a	6 s,a	10	2
Anas querquedula Garganey	0	3 b,a	2 s,a	5	7
Anas acuta Pintail	2	1 a	5 a	8	4
Fulica atra Coot	0	3 b,a	5 a	8	4
Anas crecca Teal	+	1 a	7 a	8	4

which has caused a decline in the populations of macrophyte depending, herbivorous waterfowl (Blindow *et al.* 1993).

Table 1 shows the degree of dependence on agricultural land and natural habitat for different species of herbivorous waterfowl from the western Palearctic. Mute Swan *Cygnus olor*, Bean Goose *Anser fabalis* and Greylag Goose spend on average nine months per year on agricultural land. Ten out of 16 considered species are confined to pasture or arable land for five months or more. The use of agricultural habitat is related to body size; the large species spend more time on agricultural habitat than smaller species $r_s = 0.94$, $P < 0.001$. In other words, only the small herbivores still rely on natural habitat for the greater part of the year.

The present winter distribution of herbivorous *Anatidae* in Western Europe is closely linked to the presence of improved grasslands (Owen 1976, Rutschke 1987). As a consequence of the high stocking rates of domestic animals, ammonia volatilisation occurs. From a total anthropogenic NH_3 emission in Western Europe of 4 Mt year^{-1}, 2.5-3.0 Mt year^{-1} originated from domesticated animals (ECETOC 1994). Figure 3A shows the isoclines of NH_4-N as measured in precipitation all over Europe as an indication of the large-scale presence of highly improved grasslands (Schaug 1994). As most of the volatilised NH_3 is supposed to precipitate quickly (Schaug 1994), the pattern represents local emission rather than the effect of atmospheric transportation as in other compounds. The distribution of the highest goose concentrations in Europe in winter closely coincides with this pattern (Fig. 3B), pinpointing the prominent position of the Netherlands as well as the area around the Black Sea in Russia. Also for herbivorous ducks and swans this pattern fits, as is shown by the European January census data com-
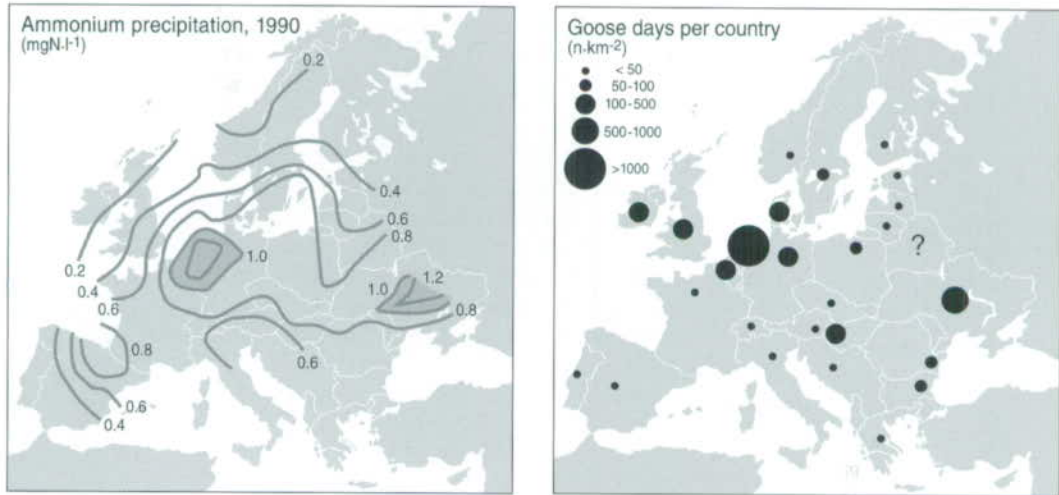
Figure 3. (A) Isoclines of NH_4 deposition in Europe according to Schaug (1994) as a measure for the degree of intensification of agriculture. (B) Distribution of the total number of geese in Europe expressed as density in agricultural habitat calculated from data in Madsen (1993), J. Madsen *in lit.* extended for Ukraine by M. Zhmud.

piled by Rose and Scott (1994). Because of the paramount importance of the Netherlands as a wintering habitat and the fact that agricultural management is the most intensive in this country, the analysis of how bird numbers have reacted in detail to changes in agricultural practice will be limited to this country.

Present distribution in the Netherlands

Figure 4 shows the typical distribution of the different species over Dutch territory in January 1993. Brent Geese are extremely coastal in their distribution and Wigeon *Anas penelope* is concentrated in the moist peat meadows in the provinces of North and South Holland. Barnacle Geese consist of both coastal and inland feeders, but the species is limited to a fairly restricted number of sites compared to White-fronted Geese, which are also present in the area of the large rivers. Greylag Geese in winter are using the estuarine areas in the southwest of the Netherlands. The conclusion from this pattern is that, except for the grassland and agricultural areas on sandy soils, waterfowl use most of the agricultural areas in the alluvial and coastal parts. The distribution of roosts, which is merely limited to these parts as well, may be of additional importance in explaining this distribution. The possibility that soil type influences grassland quality is less likely to be of importance due to the equalising effect of the soil adjusted nitrogen application (Van Steenbergen 1977).

Numerical response in the Netherlands

From the 17 species listed in Table 1, 13 have peak numbers while wintering, one during autumn migration (Greylag Goose) and one during spring migration (Brent Goose, Ebbinge 1992). Two species, Garganey and Shoveler, are present in highest numbers during summer. Because long-time series from this period are lacking, the latter two have been excluded from the analysis. For the dabbling ducks the January count was in most years the only country-wide survey. For geese and swans several counts were available from which the highest was used. The negative effect of harsh winters on waterfowl is well known, especially on the dabbling ducks and Coot *Fulica atra* (Ridgill & Fox 1990).
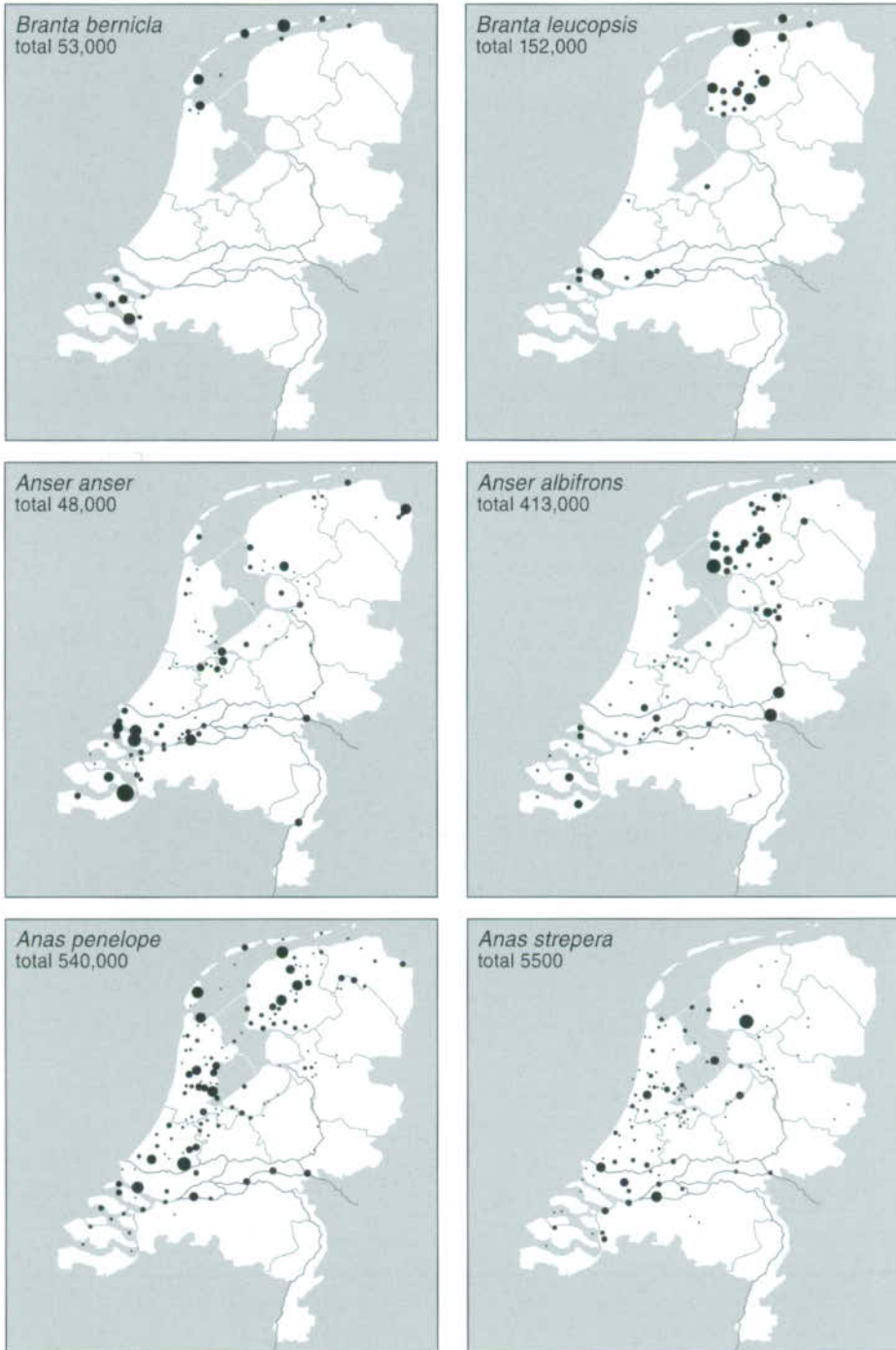
Figure 4. Distribution of several species of herbivorous *Anatidae* in the Netherlands, January 1993 after Van Roomen *et al.* 1994. Scaling of dots is relative to maximum number per species. This mild winter shows the typical pattern of use of grasslands and arable land in the lower part of the country with main points in distribution slightly differing among species.

Therefore, the severe winters of (January) 1963, 1970, 1979, 1982, 1985, 1986 and 1987 were excluded from these groups. The dabbling duck numbers have been calculated for each year, correcting for uncounted sites. As described by Buesink *et al.* (1992) and Beintema *et al.* (1993), the method based on "inputting" of missing values reveals the best estimate for the total numbers present in a particular year. This way gives the best extrapolation of the numbers really present in the Netherlands. A total of 1200 sites is thus available of which 332 are internationally important wetlands. For the geese and swans which were more or less integrally counted at their feeding grounds each season, the actual recorded numbers were used (Ganzenwerkgroep 1976-1992, Van Roomen *et al.* 1994). Figure 5 shows trends for 13 species, presented in combination with comparable ecological groups.

Mallard, Pintail *Anas acuta* and Teal *A. crecca* fluctuate around a factor five, but these species of dabbling ducks show no overall trend. Coot shows a gradual increase of 2.3% *per annum* from 1967-1980, levelling off and perhaps slightly declining afterwards. Wigeon shows a significant increase in numbers over the entire period. From a mere 100 000 birds during the late sixties and an increase of 11.4% *per annum* during the 1970s, up to 800 000 were on average estimated in the late 1980s. However, the rate of increase continually slows down, as is shown by the second order polynomial fitted to the data. Gadwall *Anas strepera* resembles this picture, but at much lower absolute numbers. The rate of increase, however, is at 19.7% *per annum* in the period 1970-1980 extremely high compared to the other duck species.

All five species of geese show increasing numbers over the period 1960-1990, from a factor 8 in Barnacle Goose up to a factor 30 in Brent. Barnacle Goose and White-fronted Goose show no sign of satiation in the rate of increase so far. Before 1970, Greylag Goose and Bean Goose already show a much higher increase rate than the other three species (7.6% and 5.4% compared to 1.9% (Barnacle), 0.7% (Whitefront) and -0.2% (Brent)). In the Netherlands, Pinkfeet also increased from *c.* 6500 in mid 1970s, to > 13 000 at maximum in early 1990s, *i.e.* 4% *per annum*. In November 1993 *c.* 30 000 were counted, the result of a reshuffling of goose numbers between Denmark and the Netherlands due to a rapid decline in feeding opportunities in the former country in early autumn (J. Madsen pers. comm.)

The swans also showed a continual increase in number. After a 7% annual increase between 1970-1980, the Mute Swan's numbers stabilised during the 1980s. After 1973 a sudden increase in the number of Mute Swans became apparent. Extended growth in numbers occurs also in Bewick's Swan *Cygnus columbianus bewickii*. With numbers in the same range as the Mute, the Bewick's Swan continues to increase, whereas those of the Mute Swan have completely levelled off. Whooper Swans increased at the same rate as Bewick's in the Netherlands (*c.* 400 in mid 1970s, to over 1500 at maximum in early 1990s).

Discussion

Causes of response

All species that rely heavily on agricultural habitat in winter have increased in numbers, in the Netherlands at least. This may have been a redistribution of numbers as for example in Wigeon, where numbers on a NW European level remained stable (Monval & Pirot 1989, Rose & Scott 1994, but see Rose 1995), or an actual increase in the total flyway population as in the geese. It was shown that nowadays the smaller species generally tend to rely less on agricultural food and still more on natural areas. Their numbers fluctuated but did not show any overall trend. Also Mallard, although depending for 7 months on agricultural habitat, showed no clear response over the last decades. This might be related to the aquatic way of foraging which is practised by this and other small species, thus depending more on invertebrate food as well as non-agricultural plant food than suggested by their mere presence in the
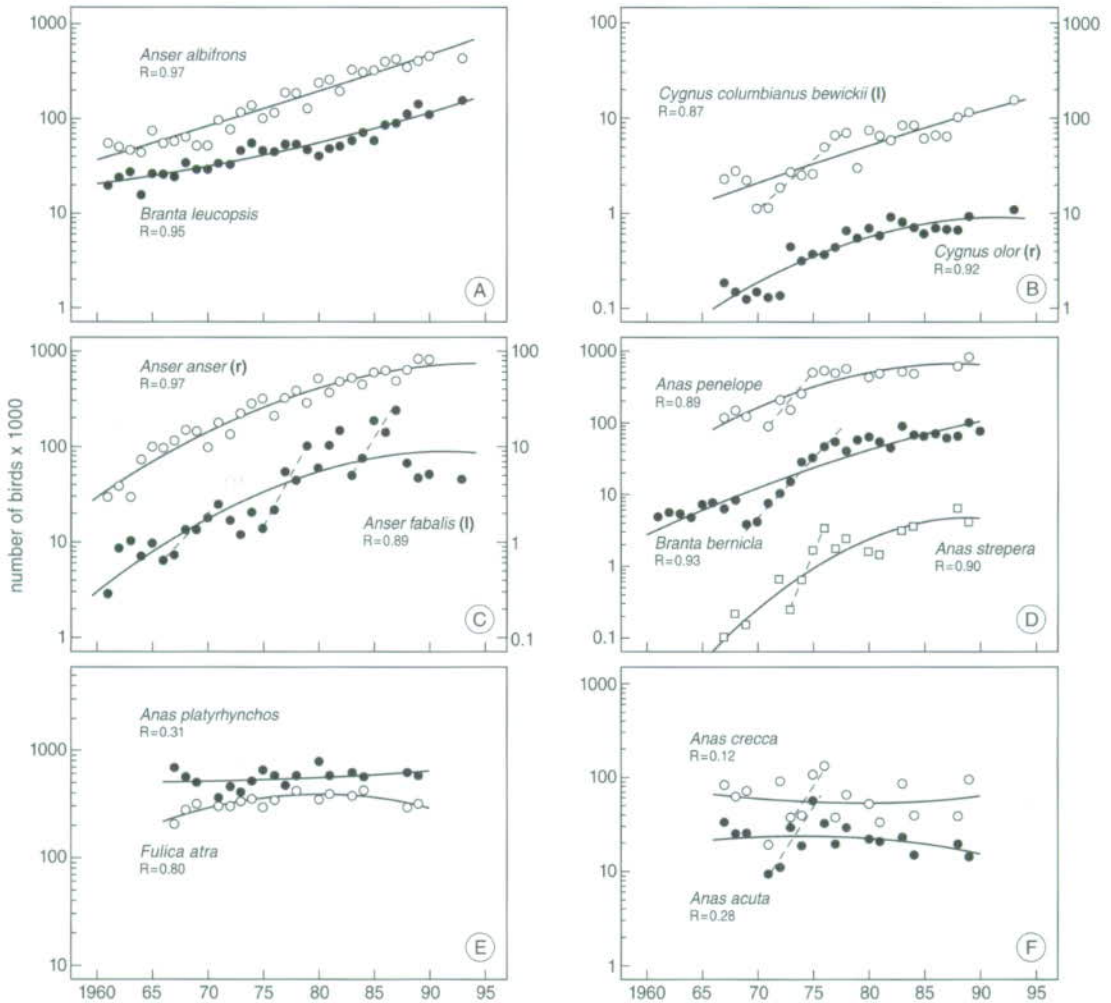
Figure 5. Change in numbers of different species of *Anatidae* in the Netherlands, combined for comparable ecological groups. For ducks and Coot *Fulica atra* harsh winters have been omitted. Numbers have been plotted on a logarithmic scale to compare changes in annual growth rate. Best fit for the data points was described by second order polynomials. For ducks and Coot mid-winter counts have been used, for geese and swans the annual maximum number. (r) right-hand, (l) left-hand scale.

habitat per se (ditches/canals). For Garganey and Shoveler no census data from the mid-winter counts were used because of a too low number compared to the annual maximum. Based on breeding census data, however, Garganey is strongly declining (85% reduction since the 1970s) and Shoveler is stable (SOVON 1987), which is in line with the conclusion that no increase is apparent in the other small species without much terrestrially taken agro-food. By contrast, Wigeon, which is a true grazer (Rijns-dorp 1986, Mayhew & Houston 1989), showed a clear response with an increase of 11% *per annum* during the 1970s. The response pattern of the Coot is somewhat ambiguous. A slow increase during the 1970s slowed down completely in the 1980s after which some lower numbers were counted. In winter this species depends both on grass, aquatic benthos and Zebra Mussels *Dreissena polymorpha*. The

decline in numbers which was observed in the years after 1985 is more likely to be associated with a decrease in the availability of *Dreissena* than with a response to a change in grassland quality (A. Bij de Vaate pers. comm.).

Timing of response

The timing of the start of use of agricultural food might be expected to be a function of body mass. As avian herbivores digest their food only superficially (Mattocks 1971), the food quality (protein, crude fibre content) proves to be of prime importance to the selection of feeding areas, specific food plants, and the relation to the timing of their annual migration (Owen 1971, 1976, Prop & Vulink 1992). Because of the gradual increase in food quality over the years, it can be expected that different species respond at different times to this change in food quality. Mute Swans have been seen foraging on pasture land from 1946 on, although numbers at that time were extremely low. Whooper Swans frequented grass-polders in substantial numbers from the 1940s on (Jonkers *et al.* 1987). According to these authors this species and Bewick's Swans were already seen in the period 1890-1910 on inundated meadows along the river Eem, where they may have foraged on uprooted grass-stolons. These species, dependent upon aquatic macrophytes, showed a delayed shift to grassland, which was related to the sudden disappearance of water plants as a consequence of the deteriorating water quality (1967-1970). Forced by this event, Mute Swan and Bewick's Swan changed food drastically in 1971/72, (Poorter 1981, 1991). Larger flocks were seen on grassland from that time on throughout the winter period. In these species, macrophyte food as tubers, stolons (winter) and leaves and seeds (summer), probably is of superior quality in relation to grass leaves (Beekman *et al.* 1991). The habit of feeding on grassland by Greylag and Bean Goose was primarily limited to wet situations along rivers and inundated polders. Bean Geese were recorded in the Eempolders near Hilversum as early as the winter 1789-90 for example (Jonkers *et al.* 1987). However, Greylag Goose and most Bean Goose, both large-bodied bulk feeders among the avian herbivores, responded later, in the 1950s with increasing numbers (Table 2). Pinkfeet have colonised the province of Friesland in greater numbers from the winter 1957/58 on (Timmerman 1977, Schilperoord *et al.* 1989). Similarly the Barnacle Goose started to arrive in greater numbers in the region of the Lauwerszee in Friesland from 1953/54 onwards (max. 2750, Timmerman 1962). Also for this species, from 1957/58 on (a mild winter), a spectacular increase was noticed (to 12-13 000 at maximum).

By contrast, the smallest species, being selective grazers such as Brent Goose, Wigeon and partly also Gadwall *Anas strepera*, did respond first during the 1970s. Brent Geese, which before 1970 only sporadically frequented grass-polders, have shifted to this winter habitat since 1971/72 (Schiermonnikoog, pers. obs). After 1973 this habit became widespread in the coastal region of the Netherlands. Much later it also happened further east in Schleswig Holstein and Niedersachsen (from 1983 on, Prokosch 1991). This shift to pasture meant the relief of a food bottle-neck which existed up to then between the moment of depletion of the Eelgrass *Zostera* spp. beds in France and Britain in December/January, and the start of growth of the saltmarsh vegetation in the Wadden Sea area in April. Wigeon also responded at the same time at a comparable rate as observed in Brent (Table 2). These species often used to winter in association with Brent, feeding on *Zostera* and macro algae. Starting in 1970/71, Wigeon began to winter in greater numbers on the moist, peaty grasslands of Friesland and Noord and Zuid Holland. From the late 1980s Wigeon can be seen grazing on artificial grasslands already from early October on. This pattern differs greatly from that recorded earlier, with peak numbers present on inland polder grass not before December-January (Van Eerden 1984). At that time saltmarshes were visited by the majority of birds in early autumn.

There is evidence therefore that larger avian herbivores preceded smaller species as regards the timing of response to the gradually improving grasslands. Apparently, many species responded with fast

Table 2. Increase in numbers, expressed as annual growth % for different periods, based on highest counts in the Netherlands. For dabbling ducks and swans with only limited data available before 1967 data before this have been conservatively estimated from indices presented in Eygenraam (1962) and Doude van Troostwijk (1965). Peak period shows the strongest increase over a period of at least three years in succession. Also given NW European trend during the period 1977-1986 after Monval & Pirot (1989), Madsen (1991), Rose (1995).

+ or - estimated annual increase or decrease 0-3%. ++ or - - idem 4-6% *per annum*.

Species	Annual growth				Peak of increase	Trend in Europe
	1950/60	1960/70	1970/80	1980/90		
Anser anser	++	7.6	5.4	3.0	1962-1967	increase
Anser fabalis	++	5.4	7.0	-2.0	1974-1978	increase
Branta leucopsis	+	1.9	2.0	5.0	1970-1974	increase
Anser albifrons	+	0.7	4.7	3.0	1969-1973	increase
Branta bernicla	-	-0.2	11.0	2.0	1969-1976	increase
Anas penelope	-	+	11.4	2.6	1971-1975	increase
Anas strepera		+	19.7	6.0	1971-1976	increase
Fulica atra		+	2.3	-1.1	1975-1977	stable
Cygnus columbianus bewickii			7.8	3.0	1971-1977	stable
Anas acuta		-	6.4	-1.6	1971-1975	stable
Anas crecca	+	-	4.7	1.8	1971-1976	stable
Anas platyrhynchos	-	-	2.6	-0.8	1971-1975	stable

growing numbers during the early 1970s (Table 2, Fig. 5). A series of eight successive mild winters (Oskam & Reinhard 1992) following the harsh winter of 1969/70 might be responsible for this. Hard winter weather can cause extra mortality because of starvation (Boyd 1964, Beer & Boyd 1964, Suter & Van Eerden 1992). Mild winter weather can stimulate grass growth, especially in peat areas due to mineralisation of organic matter (Van Steenbergen 1977). Moreover, we hypothesise that the shift of Brent and Wigeon to improved grassland could have meant a higher survival because of better feeding conditions. As pointed out by Rooth *et al.* (1981) and Ebbinge (1985, 1991), a drop in mortality rate was demonstrated for White-fronts and Brent. These authors state as the key factor of this reduced mortality the ban on hunting in spring on White-fronts in the Soviet Union (after 1970) and year-round on Brent in Denmark (after 1972). However, the pattern compares reasonably well with that of the Barnacle Goose breeding in the Russian arctic (Fig. 5), a species not associated with marked changes in hunting practice, but which also shows remarkable deviations from the fitted polynomial in the early 1970s. Perhaps even more illustrative with respect to the effect of hunting are the cases of Wigeon and Gadwall (Fig. 5). The parallel with the pattern in growth rate of the Brent was mentioned before and these species were neither subject to marked changes in reproductive rate nor to marked changes concerning the legislation of the hunt. What remains is the effect of the series of mild winters during the 1970s and the shift from coastal to inland feeding on improved grasslands. Beside the weather, the habit of reseeding of grasslands became established in agriculture in this period. Until 1960 less than 2% of the total area was reseeded annually, from 1960-1970 less than 4% and after 1970 this rose to more than 10%, being 150 000 hectares *per annum* (Sibma & Ennik 1988). Reseeded grasslands suffer less from low temperatures (Keuning *et al.* 1988) and have a higher crude protein content at the same applied nitrogen levels (Sibma & Ennik 1988).

We do not wish to deny the apparently major effect of hunting kills on the population levels of some waterfowl species. It is unavoidable, however, to also stress the importance of winter feeding conditions as a driving mechanism behind a better survival during winter. If true, then the observed reallocation of Wigeon to high quality inland areas in the Netherlands in the 1990s is expected to be the first step towards an increase in the population level as well, provided the high levels of nitrogen application continue. In a recent analysis, Rose (1995) found an increasing trend in this species on the flyway level indeed, which is in line with our hypothesis.

Future developments by reconstruction of the past?

As we have shown, the continual process of intensification has resulted in a clear numerical response in 13 species of avian herbivores. Except for Mute Swan and the majority of Mallard, which are resident breeders in the Netherlands, all other considered species which are increasing in the Netherlands, are migrants, breeding mainly in northern Scandinavia, Spitsbergen and Russia (Perdeck & Clason 1982). Their total population is either increasing or stable (Table 2). For the populations which are stable on a European scale, this implies that a reallocation of bird numbers has occurred on the flyway level, which is important for the interpretation of trends in the Dutch situation.

Except for three species, Barnacle Goose, White-fronted Goose and Bewick's Swan which are still in a phase of constant or even exponential growth, all other species show clear signs of satiation. It is interesting to speculate about the causes of this difference in pattern. Satiation patterns occur if some resources are limited, either in the breeding areas or in the wintering grounds. At first sight it is hardly imaginable that food availability in an agricultural habitat could ever limit the number of wintering *Anatidae* (Owen & Black 1991). However, this might, to some extent, be the case in Wigeon which depends on the availability of inundated meadows or grasslands close to open water, which they need for drinking. Similarly, Brent Geese use only improved grasslands and cereal fields close to the coast which greatly limits their distribution. Also, the use that Greylags and Bean Geese make of root crops after harvest is only limited to a short period because of ploughing up fields. Flock size and social behaviour may affect maximum bird numbers that an area can support. However, these numbers are often related to the numbers elsewhere in the same, or second best habitat. Owen and Black (1991) show for the Spitsbergen Barnacle Goose that both adult (natural) mortality rate and recruitment rate are negatively correlated with population size. These authors state that nowadays this population is regulated in the breeding area. How density dependent regulation operates and to what extent the other stop-over sites or breeding regions along the flyway are involved as well, needs further study. Especially in species where spring or autumn feeding still occurs in natural habitat, density dependent factors are likely to operate as well. In Brent it has been shown how availability of preferred foodplants varied among individuals within the same flock at a spring staging site, thus affecting body condition and thus reproductive performance in the arctic (Drent & Van Eerden 1980, Teunissen *et al.* 1985 and Prop & Loonen 1986). In the case of the Barnacle Goose population which winters in the Netherlands, the recent population expansion parallels a tremendous extension of the breeding range. Being an arctic breeder until recently, restricted breeding colonies have long been known to exist only at Novaya Zemlya and Vaygach. From the mid 1980s on the species has colonised many new settlements, not only in the same region but also along the entire flyway. From the coasts of Yugorski Peninsula, Kolguyev, Pechora Delta, Kanin and Kola along the Barents Sea in Russia (Filchagov & Leonovich 1992, Vinogradov 1994, Yu. Mineyev pers. comm.), Barnacle Geese have founded breeding colonies in the Baltic, with very successful settlements in the region of Gotland in Sweden and on the coast of Estonia (Larsson & Forslund 1994, Leito 1993). Having been a protected species for a long time throughout its range, it is not imaginary that the improved winter feeding conditions have led to the population expansion and subsequent range extension. The observed exponential growth of goose numbers in the

Netherlands is therefore likely to have attributed to the expansion of the breeding area and *vice versa*. However, in species with a vast breeding range, such as White-fronted Goose or Wigeon, only changes in population size will be noticed in the wintering area.

Are we able to forecast future developments with respect to the use of agricultural land by avian herbivores? As stated earlier the amount of nitrogen applied to grasslands will be reduced considerably. From 250-350 kg ha^{-1} year^{-1} a future level of 150 kg ha^{-1} year^{-1} is foreseen (Landbouw Economisch Instituut 1960-1993, 't Mannetje 1994). Dutch government policy aims to increase the area of farm grasslands important in nature conservation to 200 000 hectares in 2005 by offering financial compensation for the reduced yield as a result of a lowered N application and a delay of the date of first cut ('t Mannetje 1994). More grassland will be turned into maize fields as maize silage has a higher nutritive value compared to grass, it is less variable with respect to climatic influences, and it gives fewer problems with urine scorch (Ketelaars & Van Vuuren 1989). This area reduction will be approximately 40% in the year 2000 compared to 1970 (Ketelaars & Van Vuuren 1989).

Beside expected benefits for the botanical composition of the swards under a less intensive regime (Korevaar 1986), and a positive effect on the entomofauna and small passerine birds and mammals, one can argue about the effects on the grazing *Anatidae* in winter. If food quality and available area decline, we expect avian herbivores to respond to this, like they have done during the past decades. The smaller duck species and Brent Goose will react first, subsequently followed by medium sized geese and the swans. Further study will have to find out whether the expected redistribution of numbers over Western Europe will also lead to a reduction in total numbers.

Increased damage as a consequence of shift?

Figure 6 shows a somewhat idealised reconstruction of the changes in grassland quality during this
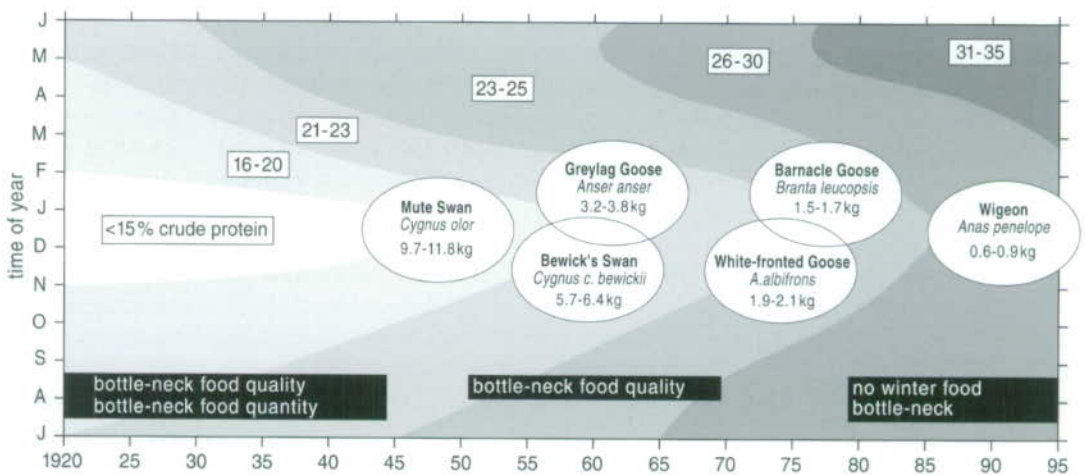
Figure 6. Approximated presentation of long-term changes in food quality of grasslands on dairy farms in the Netherlands in the course of the year. The picture shows crude protein content on dry matter base as a measure of quality. The somewhat idealised picture has been derived from data indicating the shift in date of first and last cut over the years as well as the seasonal pattern of crude protein content in fertilised and unfertilised swards (*cf.* Brandsma 1954, Kleter 1961, Keuning 1974, Sibma & Ennik 1988 and see Fig. 2A for data during winter months and from unfertilised soils). Also indicated for different species of herbivorous *Anatidae* is start of period of full dependence on improved grassland during the winter period. Species with less body mass shifted later than larger species.

century. It is based on the shift in date of first cut (see Beintema *et al.* 1985), the extended use of grass in late autumn and the effect of nitrogen fertiliser on the quality throughout the year (Brandsma 1954, Kleter 1961, Keuning 1974, Sibma & Ennik 1988 and see Fig. 2A). As discussed before, the larger *Anatidae* responded earlier in time to the continual improvement of the grass sward than the smaller avian herbivores. One of the consequences of the greater dependence of waterfowl on agricultural food is the apparent conflict with the interests of Man. Damage by grazing geese, ducks and swans has been reported for decades, and different solutions put forward (Kear 1963b, Owen 1980, 1990, Van Eerden 1990, Van Roomen & Madsen 1993). The increased quality of the food has led to the situation that growing populations of several species no longer depend on natural food in winter. This seems particularly true for the larger species which can only be dispersed, rather than distracted from the agricultural scene. It is no solution to say that, in combination with scaring practises, the still available natural areas can support these birds (Van Eerden *in prep.*). As graminoids form the major food plants for grazing waterfowl in winter, grassland and young cereals will therefore remain important future food sources. As cereals compared to grass are much more sensitive to grazing with respect to a reduction of the yield, and the greater economic losses per hectare (Groot Bruinderink 1987), much effort has been put in research aiming at quantifying and resolving the conservation/damage conflict (Summers 1990, Patterson 1991, McKay *et al.* 1994, W. Teunissen *in prep.*). One of the obvious aims is the distraction of geese and ducks from cereals and the attempt to concentrate them on less vulnerable pastures. This approach can only be successful if the energetic return of grass for the grazing birds is equal or higher, and this is only the case at a high level of fertilisation of the grass sward. The reduction in nitrogen application to grasslands which is a governmental goal is likely to further increase the difference in quality, which means an increasing risk of damage to cereals. Also, the change in the management of nature areas by a ban on cattle grazing, partly set by the lower number of cattle available, leads to a deterioration of the composition of wet meadow and saltmarsh vegetation and will unavoidably result in a greater risk of damage to cereals in the coastal regions of the countries bordering the North Sea. Especially the smaller species such as Wigeon, Brent and Barnacle Goose will be forced to concentrate both on winter cereals and on the remaining high quality pastures in future, as their demand for protein is higher than in the larger species such as Greylag Geese and Bewick's Swans (Van Eerden & J. Th. Vulink unpubl.). As outlined before, the route back to lower N-levels is uncertain. The selection of more productive strains of grass in recent years for instance, may partly buffer the effect of decreased quality of the nutritive value at lower levels of nitrogen fertiliser applied. More research is necessary to explore this field before quantitative predictions can be made about the risk of increased damage due to waterfowl grazing.

Acknowledgements

Agricultural crops attract many herbivorous water birds: (A) Harvest of cereals, Flevoland, August 1983, (B) Fertilised grassland near Edam, October 1994, (C) Spring Barley, grazed by Greylag Geese *Anser anser*, Flevoland EZ136, 8 April 1989.

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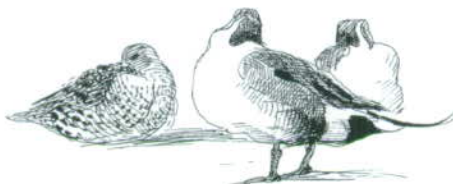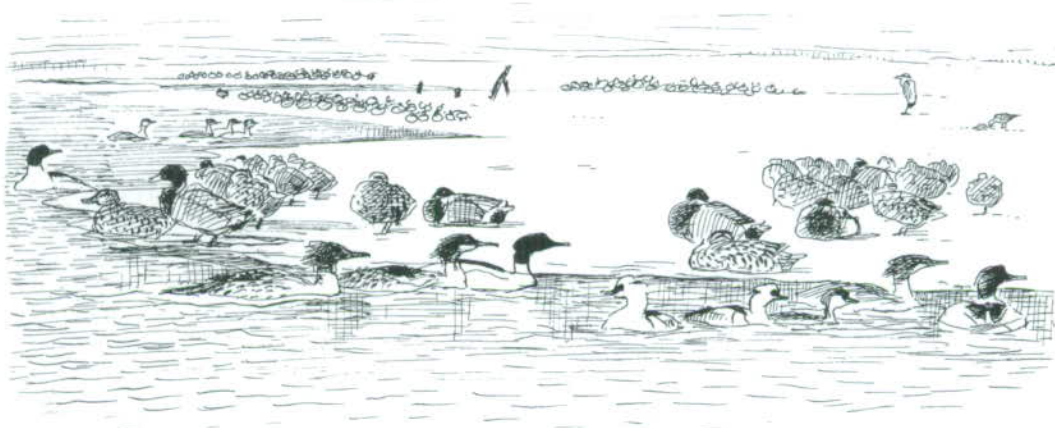
Chapter 4

Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat: energetic implications of living in a strong cooling environment

CONSTRAINTS

Jan de Vries en Mennobart R. van Eerden

Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat: energetic implications of living in a strong cooling environment

Thermal conductance of carcasses of 14 aquatic bird species was determined by the warming constant technique. The effect on thermal conductance of body mass, age, sex, fat deposits, and the degree of contact with water were studied. Only body mass and the degree of submergence in water had an effect. A negative exponential relationship between body mass and thermal conductance was found. Water contact increased the thermal conductance by a factor of 2.2 during swimming and a factor of 4.8 during diving. Leaving the water in order to reduce thermoregulatory costs is put forward as a behavioural option that might make several aquatic birds more flexible in adjusting their feeding time to meet increasing energetic requirements. Not being able to leave the water has obvious implications for both breeding and winter distributions for different-sized aquatic birds.

Introduction

Endothermic aquatic animals might be seriously affected by the thermal properties of water, because the heat capacity of water is 25 times greater than that of air. Heat loss of animals is dependent on their exposed surface area, thermal conductivity (C), and the difference between ambient temperature (T_a) and body temperature (T_b). One may wonder how birds cope with the problem of thermoregulation in their aquatic environment, because adaptation to a greater heat loss in water is not achieved by a beneficial surface-to-volume ratio such as large sea mammals have. Many bird species (*e.g. Gaviidae, Podicipedidae, Anatidae, Alcidae* and *Spheniscidae*) tolerate near-freezing water temperatures despite their small body size (Atkinson-Willes 1976, Cramp *et al.* 1977, Owen 1980). If thermal adaptation to the great cooling power of water exists, one might expect a lower C in air for aquatic bird species compared with terrestrial species. However, some studies indicate higher C in air for aquatic bird species (Bech 1980). Very little is known about actual C of birds while floating or diving. A few studies report increased C in birds while floating or diving that is two or five times their air C, respectively (Kooyman *et al.* 1976, Stahel & Nicol 1982, Jenssen *et al.* 1989). The lack of data about heat loss of birds in air and water inspired us to measure C over a wide range of species. Experiments were conducted comparing the C of birds in a standing posture in air, a partially submerged swimming posture, and a wholly submerged diving posture. In addition to the effect of body mass (m), effects of sex and age on C were also studied.

Material and Methods

In this study we used 113 carcasses of 14 aquatic bird species that were collected from the freshwater lakes IJsselmeer and Markermeer and the adjacent reed marsh, Oostvaardersplassen, in the Nether-

lands (for detailed information, see Appendix). The carcasses were obtained from local fishermen from August to March. The diving ducks (*Aythya* spp.), grebes (*Podicipedidae*), mergansers (*Mergus* spp.) and cormorants (*Phalacrocoracidae*) had been drowned accidentally in fishing gear. Only freshly caught birds with intact and entirely down-dry plumage were used. Dabbling ducks and geese (*Anas* spp. and *Anser* spp.) were collected during a *Clostridium botulinum* epidemic in the reed marsh, where the birds had died a few hours after drinking the contaminated water.

After collection, the birds were cleaned if necessary. Their plumage was dried for 2 h in a forced ventilated oven at 30 °C. After plumage drying the birds were used for experiments or were individually stored in tied plastic bags in a freezer at -20 °C until measurements began. The carcasses were stored at -20 °C, because in Tufted Ducks *Aythya fuligula* and Great Crested Grebes *Podiceps cristatus* no effect of storage for 2 months was found on C compared with direct measurement (*t*-test; Tufted Duck df = 16, $P = 0.39$, not significant [NS]; Great Crested Grebe df = 10, $P = 0.22$, NS).

Carcass masses ranged from 0.25 to 3.5 kg. Birds were aged and sexed by gonadal and plumage inspection distinguishing between juvenile (first winter) and adult (after first winter).

Whole-body C's were obtained by a warming curve analysis of the carcasses (Morrison & Tietz 1957, Herreid & Kessel 1967). Thermal conductance was expressed relative to m and not surface area, because surface area is difficult to obtain in the swimming and diving postures. Thermal conductance (kJ °C^{-1} h^{-1} kg^{-1}) was estimated by multiplying the warming constant with the specific heat of mammalian tissue (3.47 J g^{-1}; Morrison & Tietz 1957). Warming constants were obtained from the slope of the natural logarithm of the difference between T_b and T_a (ln $(T_b$-$T_a)$) versus time. The difference between T_b and T_a was read every 30 min in the standing and swimming experiments but was read every 15 min in the diving experiment. The time interval over which C's were computed was 7, 5, and 3.5 h in the standing, swimming, and diving postures, respectively. The difference between T_b and T_a was continuously recorded with calibrated thermocouples. The thermopotential of the thermocouple was amplified by a micrograph recorder (BD7, Kipp and Sons), giving a scale deflection of 0.5 mV per 100 scale divisions resulting in an accuracy of the readings of 0.08 °C.

The measuring point of the thermocouple was inserted into the intestinal tract and placed previously as far as the liver lobes. With the aid of a small glass rod, the intestinal tract was widened to improve the insertion of the thermocouple.

The C's were measured in an unventilated, isolated room in the central part of the laboratory that had a constant air temperature of 20 °C. In this room the maximal temperature change of the air that could occur during the experiments was 0.2 °C 12 h^{-1}. Change in air temperature was checked every hour from the start to the end of an experiment. The air and water temperatures were read to the nearest 0.05 °C with a mercury precision thermometer (Landsberger; 18-35 °C).

Thermal conductance of the carcasses was measured in air and then in water while swimming and diving. For 112 birds C was measured in air. For 106 birds C was measured only when standing and swimming, and for 50 birds C was measured for all three postures (see Appendix). A day prior to the experiment, the carcasses were thawed for approximately 10 h. After thawing the carcasses were cooled for 15 h in a refrigerator. Only carcasses of species weighing more than 1.5 kg were cooled longer (*i.e.* 24 h).

According to the law of Newtonian cooling and warming, the cooling or warming constant (derived as described above) is not affected by the initial temperature of the carcass but is affected by the thermal homogeneity of the carcass (Morrison & Tietz 1957). Therefore, prior to measurement carcasses were checked for their temperature homogeneity in the refrigerator by measuring the temperature in the intestinal tract from deep inside (between the liver lobes) to the anus with a precision mercury thermometer (Landsberger; -10 to 18 °C). Only carcasses that were thermally homogeneous (*i.e.* without a temperature gradient between core and skin) with T_b between 1 and 4 °C were used for measurements;

Intact body of Great Crested Grebe *Podiceps cristatus* in swimming position, used to measure thermoconductance.

otherwise, they were cooled longer. The same procedure was followed prior to taking the swimming and diving measurements.

During measurements in air at 20 °C, the carcasses were laid on their backs on a wire mesh (3 cm x 3 cm) 50 cm above a table. Tanks filled with 70 and 100 l of water were used in the swimming and diving experiments, respectively. By using large volumes of 20 °C water (in an infinite heat sink) in thermal equilibrium with the surrounding air (air temperature = water temperature) during the experiments, changes in water temperature due to the cooling effect of the cold carcasses are then insignificant (0.01 °C or less). The carcasses were fixed in the swimming posture by clamping their heads above the water when they were floating on the surface. The heads and legs of the carcasses were tied to rods attached to a table standard to keep them in the diving posture (head downward, body vertical, tail 15 cm below the water surface). Carcass and standard were placed under water in the 100 l tank. Water was prevented from leaking into the body cavities by sealing the throats and cloacae with 5 cm^3 glycerine and by taping the bills.

The fat content of the carcasses was gravimetrically determined by either the Soxhlet or the diffusion method. To improve the fat mass analyses, the thorax and abdomen were opened and the glycerine was removed from the throat and cloaca. The diffusion method gave reliable results in birds with m's up to 1.5 kg. Therefore, the diffusion method was only used in these birds. The Soxhlet method was used in birds with m's greater than 1.5 kg. Oven-dried carcasses (2 d at 100 °C and 5 d at 80 °C) were weighed before and after fat extraction to obtain the fat and fat-free masses. We dried at these temperatures because drying at 100 °C in chickens (Kirkwood 1981) and 95 °C in rats (Leppington *et al.* 1978)

did not reduce the fat content by causing loss of volatile components soluble in petroleum ether. In addition, Kirkwood (1981) found that in samples dried for 8 d at 60 °C to constant weight, dry matter content was overestimated by residual water. In the diffusion method the carcasses were soaked in petroleum ether, and the fat masses of 30 carcasses were determined per session. Therefore, the carcasses were individually placed in loosely woven nylon bags to keep them separate during the fat extractions. The diffusion method was carried out in five extraction steps. In each step 20 l of petroleum ether was used per 30 carcasses. The first fat extraction step was performed in petroleum ether that had been used four times previously. The second extraction step was performed in petroleum ether used three times previously, and so on. The fifth and final fat extraction step was performed in clean petroleum ether. The total time of the five diffusion steps was 7 d. The first four extraction steps took 1 d per step, and the fifth and final step took 3 d. After fat extraction the carcasses were dried in a vacuum oven at 60 °C at a pressure of 3-5 cm Hg for 24 h and weighed to the nearest 0.1 g. Fat masses (g) obtained by the diffusion method were corrected with the following regression: fat $mass_{Soxhlet}$ = fat
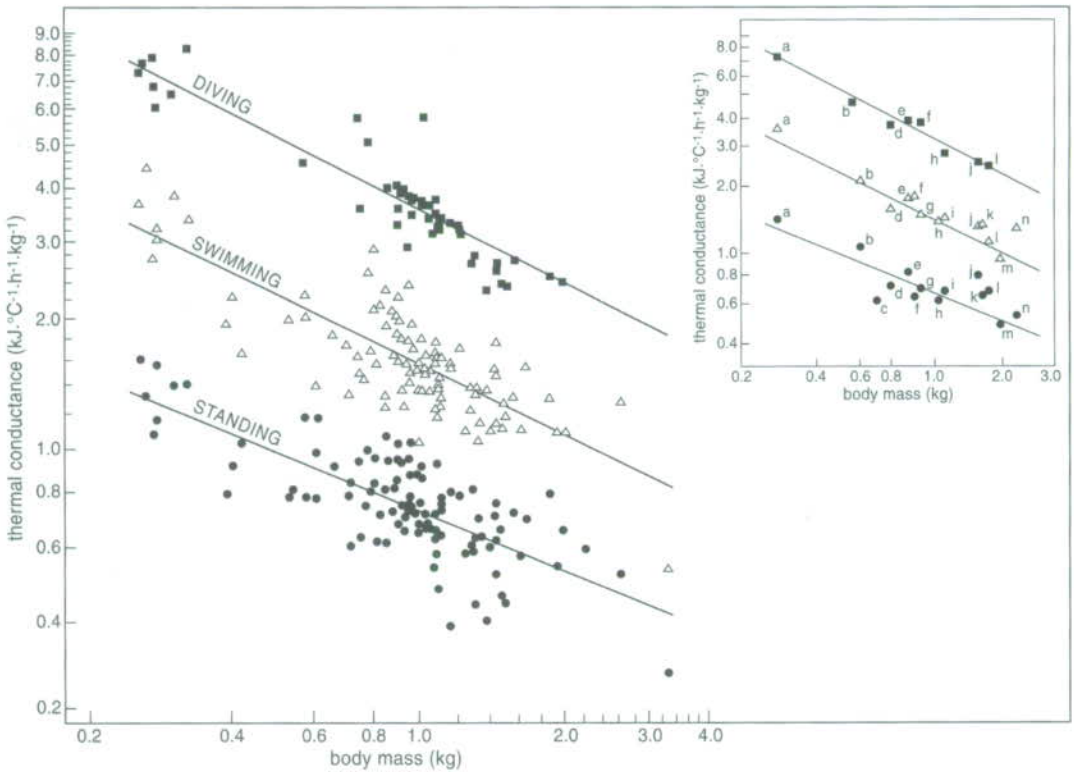
Figure 1. Relationship between m (kg) and C (kJ °C^{-1} h^{-1} kg^{-1}) in various aquatic birds. Thermal conductance was measured for the standing posture in air (filled circles), for the swimming posture (open triangles), and for the diving posture in water (filled squares). The lines represent $C = am^b$ obtained from regression of log (C) on log (m) for the standing posture in air ($C = 0.705m^{0.461}$, $R^2 = 0.577$, $SE_{slope} \pm 0.038$, $P < 0.00001$, $N = 112$), swimming posture in water ($C = 1.532m^{0.546}$, $R^2 = 0.656$, $SE_{slope} \pm 0.039$, $P < 0.00001$, $N = 106$), and diving posture in water ($C = 3.47m^{0.573}$, $R^2 = 0.828$, $SE_{slope} \pm 0.038$, $P < 0.00001$, $N = 50$). Species values (mean of C) are presented in the inset Figure: a. *Anas crecca*; b. *Mergus albellus*, c. *Fulica atra*; d. *Bucephala clangula*; e. *Aythya fuligula*; f. *Anas platyrhynchos*; g. *Podiceps cristatus*; h. *Aythya marila*; i. *Mergus serrator*; j. *Gavia stellata*; k. *Mergus merganser*; l. *Somateria mollissima*; m. *Anser anser*; n. *Phalacrocorax carbo*.

mass$_{\text{diffusion}}$ × 1.0344 + 2.2790 ($N = 61$, SE$_{\text{slope}} = 0.01261$, $R^2 = 0.991$). This regression was obtained from 61 carcasses (0.2-1.5 kg) for which the fat mass was first determined by the diffusion method followed by the Soxhlet method.

Descriptive statistics, regressions, and F-tests were determined according to Sokal and Rohlf (1981).

Results

Thermal conductance was positively correlated with the degree of contact with water. In Table 1 the average C's of the various species, age, and sex classes found for the standing posture in air and the swimming and diving postures in water are sorted according to increasing m. The respective C's of the swimming and diving postures were 2.0-2.5 and 4.8-5.0 times the value of the standing posture in air.

For each posture allometric relationships between m and C were calculated to obtain the interspecies lines (Fig. 1). A strong negative exponential relationship between m and C was found for all three conditions (Fig. 1). The allometric functions of the swimming and diving postures showed the same magnitude of elevation relative to the standing posture in air, as mentioned previously (Table 1). The slopes of the three lines are not significantly different from each other (F-test), but the y-intercepts are statistically different (ANCOVA, $P < 0.00001$).

The allometric relationships between m and C did not differ significantly between the age and sex classes in each posture (F-test; Table 2).

A within-species analysis was carried out for *Podiceps cristatus*, *Aythya fuligula*, and *Aythya marila*. Also within species, C decreased significantly with increasing body mass, but regressions were not significant for *Podiceps cristatus* and *A. marila* in air (Fig. 2).

The fat fraction of fresh m varied between 5% and 25% for more than 95% of the birds measured. This range was typical for the annual variation for the species occurring in the study area. Regressions of the residuals for fat against residuals of C were far from significant for the three postures (Table 3). In addition, we looked for a more general effect by placing the residuals in a contingency table. The analyses of cell frequencies by chi-square tests were not significant for all three postures (standing, $P < 0.8$; swimming, $P < 0.2$; diving, $P < 0.15$). This indicates that no relationship exists between fat content and C.

Discussion

Measurements of intact carcasses of aquatic birds with the warming constant technique indicated that m was an important factor influencing the level of the dry C in air and water. For practical reasons we used the warming instead of the cooling technique. The direction of heat transfer is unlikely to influence its speed, which has been demonstrated by Morrison and Tietz (1957) in a heat transfer study on three vole species. Warming or cooling of carcasses revealed the same heat transfer coefficient in these voles. Therefore, our data are completely comparable with the heat transfer data obtained with the cooling constant technique of Herreid & Kessel (1967) on Alaskan terrestrial birds.

The present study is in agreement with the results of others that C decreases with increasing m (Herreid and Kessel 1967, Drent & Stonehouse 1971, Kendeigh *et al.* 1977, Aschoff 1981). These studies present C as an allometric function of m such that $C = am^b$, where b is -0.536, -0.479, -0.484, and -0.411, respectively. The value of $b = -0.461$ for the aquatic birds in our study is in good accordance with b's from the former studies. However, their corresponding values of a (in $C = am^b$; -0.474, -0.430, -0.332, and -0.462, respectively) are 1.5-2.0 times lower than the value of a (*i.e.* -0.705 for standing

Table 1. Thermal conductance for different species, age, and sex groups measured in three different postures.

Species	Age, Sex[a]	N	m[b] (kg)	C[c] (kJ °C^{-1} h^{-1} kg^{-1})			Ratio to Standing				
				Standing	Swimming	Diving	Standing		Swimming		Diving
Anas crecca	A, F	4	.279 ± .015	1.46 ± .07	3.66 ± .27	7.27 ± .45	1	:	2.5	:	5.0
Bucephala clangula	A, F	4	.758 ± .029	.68 ± .04	1.48 ± .08	...	1	:	2.2	:	...
Aythya fuligula	J, F	5	.834 ± .039	.83 ± .08	1.92 ± .26	...	1	:	2.3	:	...
A. fuligula	A, F	5	.922 ± .061	.85 ± .04	1.67 ± .14	...	1	:	2.0	:	...
Podiceps cristatus	J, M	4	.939 ± .037	.70 ± .02	1.65 ± .16	...	1	:	2.3	:	...
A. fuligula	A, M	10	.946 ± .035	.77 ± .03	1.68 ± .06	3.71 ± .24	1	:	2.2	:	4.9
P. cristatus	J, F	4	.994 ± .067	.70 ± .06	1.48 ± .06	3.37 ± .10	1	:	2.1	:	4.8
P. cristatus	A, M	6	1.115 ± .098	.68 ± .04	1.38 ± .08	3.40 ± .20	1	:	2.0	:	5.0
Aythya marila	A, F	4	1.198 ± .047	.61 ± .09	1.33 ± .06	2.94 ± .16	1	:	2.3	:	4.8
Mergus serrator	A, M	4	1.314 ± .031	.63 ± .03	1.31 ± .10	...	1	:	2.1	:	...
A. marila	A, M	5	1.431 ± .022	.50 ± .05	1.28 ± .06	2.41 ± .07	1	:	2.5	:	4.8

Note. Ellipses indicate $N < 4$ for the posture.

[a] A = adult, J = juvenile, M = male, and F = female

[b] Values shown are means ± 1 SE.

[c] Values shown are means ± 1 SE if $N \geq 4$.