

Individual Differences in Feeding Habits in a Newly Established Great Egret *Casmerodius albus* Population: Key Factors for Recolonisation

Authors: Voslamber, Berend, Platteeuw, Maarten, and Eerden, Mennobart R. van

Source: *Ardea*, 98(3) : 355-363

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.098.0309>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Individual differences in feeding habits in a newly established Great Egret *Casmerodius albus* population: key factors for recolonisation

Berend Voslamber^{1,2,*}, Maarten Platteeuw¹ & Mennobart R. van Eerden¹

Voslamber B., Platteeuw M. & van Eerden M.R. 2010. Individual differences in feeding habits in a newly established Great Egret *Casmerodius albus* population: key factors for recolonisation. *Ardea* 98: 355–363.

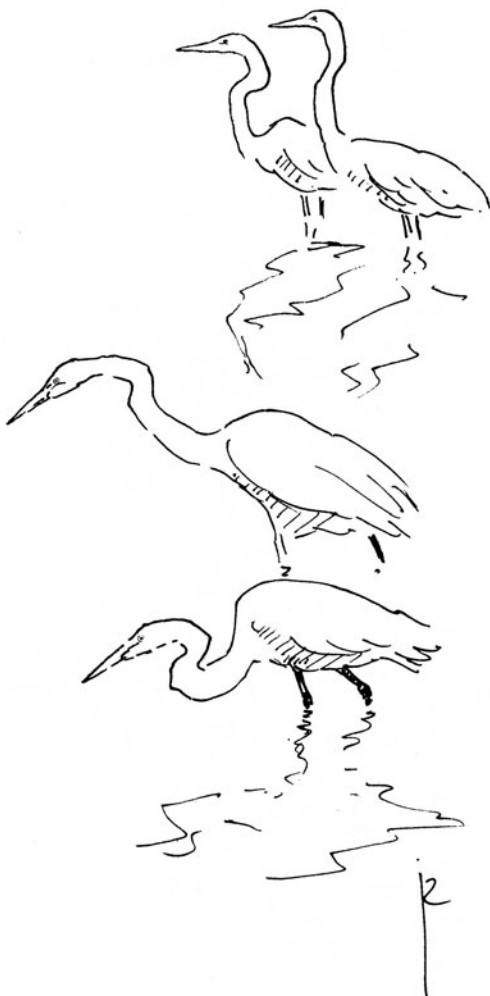
After having almost completely vanished from The Netherlands by the 19th century, from the 1970s onwards the Great Egret is increasing in numbers again, particularly in the newly created wetland of Oostvaardersplassen. During the first 25 years, the rate of re-colonisation has been extremely low, the resident population never exceeding five breeding pairs. From 2000 onwards, however, following the extension of the surface area of shallow marshland, the number of breeding birds increased to 45 pairs. This paper deals with the feeding ecology of the Great Egret during 1976–99, when numbers were at a low level. Individual differences in food choice and feeding habits were studied in order to gain insight into the key factors for establishing and maintaining a healthy population. Observations on foraging birds were carried out during 1987–92. The birds foraged mostly within the reserve. From March to July they preferred foraging in ditches, changing to Reed borders of shallow pools and dry grasslands from August onwards. In the ditches, Three-spined Stickleback *Gasterosteus aculeatus*, other small fishes and tadpoles were the main prey (91.4% of all prey items). In the shallow water bodies the egrets caught almost exclusively sticklebacks, and in grasslands Common Voles *Microtus arvalis*. One bird was observed feeding near fishing boats, taking Perch *Perca fluviatilis* and Roach *Rutilus rutilus* of 10–20 cm length. When feeding on sticklebacks, a Great Egret had to forage for 1.5 to 3 hours to fulfil its daily needs. When scavenging on larger fish around fishing boats only 15 minutes sufficed, but the energy expenditure was likely to be higher due to commuting flights and interspecific competition with Grey Herons *Ardea cinerea*. However, for the majority of Great Egrets the shallow and transparent water in ditches and pools with a high abundance of young sticklebacks and some coverage with emergent vegetations proved to be the most profitable feeding habitat. The decisive factor underlying the spectacular increase in recent years has probably been the creation of clear and shallow freshwater pools and inundated grasslands in the formerly dry border zone of Oostvaardersplassen. These foraging grounds lie close to undisturbed breeding sites. This finding may prove useful for wetland restoration elsewhere in The Netherlands.

Key words: *Casmerodius albus*, Oostvaardersplassen, prey choice, feeding technique, intake rate, habitat reconstruction

¹Rijkswaterstaat Waterdienst, P.O. Box 17, 8200 AA Lelystad, The Netherlands;

²present address: SOVON Dutch Centre for Field Ornithology, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands;

*corresponding author (berend.voslamber@sovon.nl)



The Great Egret *Casmerodius albus* has a worldwide distribution, inhabiting large parts of Europe, Asia, Africa and the Americas (Cramp & Simmons 1977, Del Hoyo

et al. 1992). As a consequence of the drainage and fragmentation of most large wetlands in Europe (van Turnhout *et al.* 2010), the distribution is nowadays

limited. Until recently, the most north-western breeding place in Europe was the Neusiedlersee in Austria (Dick *et al.* 1994). During the early 1990s new breeding grounds have been colonised in Italy, France and Spain (van der Kooij & Voslamber 1997).

In The Netherlands the species may have bred in the Middle Ages (Brouwer 1954). During the 19th century, however, it was only recorded occasionally. Apparently, the Great Egret had vanished from the Dutch freshwater wetlands in much the same way as other formerly abundant large marshland bird species that depend on large-scale breeding and feeding areas (e.g. Dalmatian Pelican *Pelecanus crispus*, Black-crowned Night Heron *Nycticorax nycticorax*, Squacco Heron *Ardeola ralloides* and Little Egret *Egretta garzetta*; Brouwer 1954, van Eerden *et al.* 2010). Until the early 1970s, the Great Egret was still considered a rare vagrant in The Netherlands. From 1975 onwards, the species has been observed annually – in later years also as a breeding bird – with increasing frequency and in increasing numbers in the nature reserve Oostvaardersplassen, a newly created wetland of some 5600 ha (Vera 1988).

In order to gain insight into the factors that may have been responsible for this development, this paper will highlight observations on the feeding ecology of the small population of the Great Egret in Oostvaardersplassen during the early years of settlement. Special attention was paid to individual differences in prey choice, feeding techniques and selection of feeding habitats, and to the consequences of these differences for the individual birds' energy budget and reproductive behaviour. The relationship between induced water level fluctuations, as a feature of natural dynamics related to larger wetland areas, and foraging and breeding success will also be discussed.

STUDY AREA

The nature reserve of Oostvaardersplassen consists of a freshwater marsh of 3600 ha and a well-drained border zone of 2000 ha (Fig. 1). The area is situated along the borders of lake Markermeer in the polder Zuidelijk Flevoland which was reclaimed in 1968. The marsh is characterised by large Reed *Phragmites australis* beds, interspersed with turbid water bodies with a depth of 40 cm on average. The water level of the marsh can be regulated artificially and was kept high in spring in order to create predator-free conditions for ground-breeding birds like Eurasian Spoonbill *Platalea leucorodia* and Greylag Goose *Anser anser*, and also for the

thousands of moulting, and thus flightless, Greylag Geese in May and June. From early July onwards the water level was artificially lowered to 30 cm or less to attract waders. The soil consists of clay with marine deposits.

From 1987 until 1991, the western part of the marsh had been artificially desiccated in order to allow the Reed vegetation to recover from erosion and heavy grazing of up to 60,000 moulting Greylag Geese (Loonen *et al.* 1991, Dubbeldam & Zijlstra 1996). This draw down resulted in an increase of shallow and clear freshwater habitats and inundated Reed beds of about 600 ha with respect to the preceding years (Fig. 1). From 1991 onwards, water levels have started to rise again in this part of the marsh (Beemster 1997). In the eastern part, the water level regime has experienced little change since 1987. Turbidity of the water within the marsh changes in accordance with droughts and excessive rainfall.

During the years of the field study (1987–92), the well-drained border zone south of the marsh consisted of grassland, well-drained reed land, Elder *Sambucus nigra*, willow bushes *Salix* spp. and Lucern *Medicago sativa* parcels (Fig. 1). In spring 1997, many shallow pools and ditches were excavated, generally holding clear water with little vegetation. Part of the grassland area was inundated with clear water during winter and spring in order to create favourable feeding conditions for waterbirds in spring. During 1987–92, the western part of the border zone (c. 650 ha) was grazed by Heck cattle *Bos taurus* (0.1–0.3 animals/ha) and Konik horses *Equus verus* (0.1–0.15 animals/ha) all year round. The eastern part (c. 1250 ha) was grazed by domestic cattle and horses (0.8–2.1 and 0.3–0.5 animals/ha respectively) from 1 May till 1 November (Cornelissen & Vulink 1996). By the year 1999, the redesign of the border zone, meant to increase the surface area of wetland suitable for foraging wetland birds, had been completed. Nowadays, the entire border zone is heavily grazed by Heck cattle and Konik horses, with average densities of 0.3–0.5 animals/ha, and with high (1.0 animals/ha) and still increasing numbers of Red Deer *Cervus elaphus* (Vulink 2001, Bijlsma 2008).

The field study on Great Egrets was mainly carried out in an experimental area in the border zone with a surface area of about 50 ha (including surrounding grasslands), called 'Waterlanden'. Here, ditches and pools with varying slopes and water depth had been excavated in three sub-areas with separate water level control. The water was clear for most of the time. Due to grazing and water level control the vegetation was short in some parts of the area, while other parts were

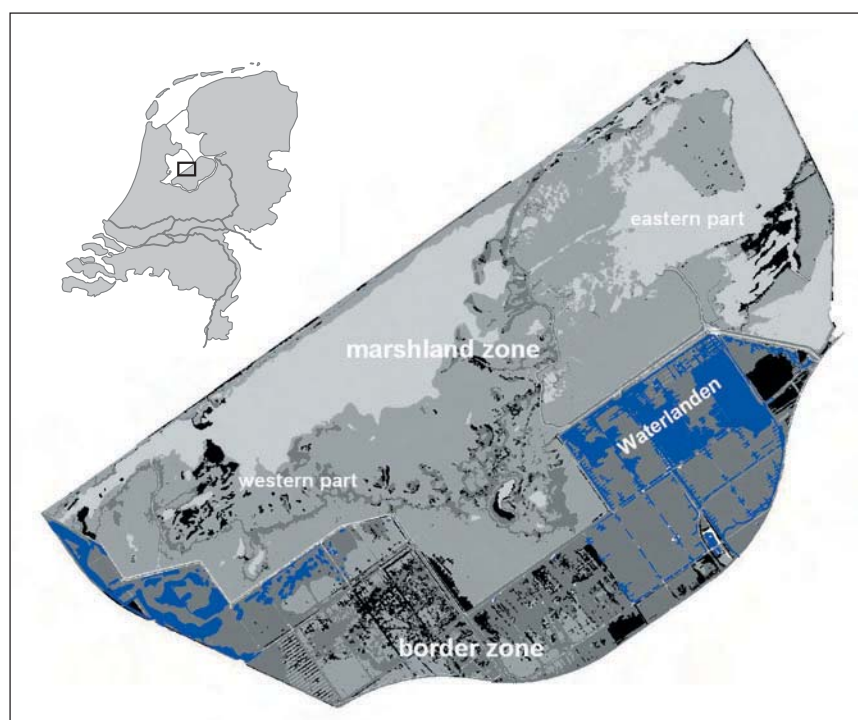


Figure 1. The Oostvaardersplassen study area; marshland zone (western and eastern parts), well-drained border zone and experimental area Waterlanden are indicated. New marsh areas are indicated in blue. Black patches represent stands of trees, mostly willow *Salix* spp. and Elder *Sambucus nigra*.

overgrown with Reed (Voslamber 1996). Within the experimental area, Great Egrets were seen feeding on fish and other aquatic prey in the ditches, as well as on Common Voles *Microtus arvalis* in the surrounding grasslands. Additional information on food was gathered in an inundated grassland in Oostvaardersplassen and along the borders of nearby Lake Markermeer.

METHODS

Since 1984, Great Egrets in Oostvaardersplassen have been counted once a month during aerial surveys. Before 1984, and later on also in the vicinity, the birds were counted mainly from dikes and roads. The estimates of breeding bird numbers were based on aerial surveys in April and May. Great Egrets were spotted from an altitude of 200–300 m. Besides recording nests, foraging egrets were counted in sub-areas in order to study habitat choice.

Most of the research on feeding ecology was carried out during 1987–92. In 'Waterlanden', observations were made from three observation towers. From each one of these towers the entire area could be checked for birds with binoculars and telescopes (20–60×). During March to August 1987–91, for 1–4 days a week, an observer used the hides for 4–14 hours per observation day. Observations were carried out from one hour before

sunrise till early in the afternoon. In September to February, the area was checked for birds at least once a week. In most cases it was possible to follow individual Great Egrets for longer periods when within a distance of up to 500 m. Prey species could be identified because the birds held the prey in the tip of their bill before swallowing. Prey size was estimated by comparing it with the length of the birds' bill (c. 12 cm; Cramp & Simmons 1977). It was assumed that prey samples taken from the same site and measured directly represented the complete spectrum of prey available to the birds, because the samples were taken in the same water layer as where the egrets were feeding in. Numbers of prey items were counted per minute foraging. Switches in behaviour (foraging, resting/preening, flying) were also noted. Additionally, in 1992 similar observation sessions have been carried out on Great Egrets feeding within the marshland zone of Oostvaardersplassen (Fig. 1). In this area, the birds were often feeding too far away from the observers, resulting in fewer observations.

We sampled fish and aquatic invertebrates with a scrape-net. Sampling took place once or twice a month over the period April–October (1987–91), during the night and only in the shallow parts of the ditches. The polyethylene net with a mesh width of 2 mm is attached to a metal frame of 50 by 100 cm at the end of a long stick. The net was pulled from the edges of the

ditches through the water body with a quick pull. The effectively sampled surface area was shown to be about 1 m² and up to 40 cm deep. Sampling took place during the night and only in the shallow parts of the ditches. Length–mass correlations for fishes and tadpoles could be made from sub-samples (Appendix 1). Caloric values (by use of a calorimeter) of most prey species were determined from individuals sampled in the experimental area. Those for Common Vole were taken from literature (Masman *et al.* 1986).

Along the borders of Lake Markermeer birds were observed while feeding on fish discards from fishing boats. Discards were taken by various gull species *Larus* spp., but also by Grey Herons *Ardea cinerea* and Great Egrets. Individual birds were located and observed for as long as possible during feeding. Number, size and species of prey were registered per minute.

RESULTS

Numbers

The first Great Egret in Oostvaardersplassen was seen in 1972. Since 1976 one or more birds have been present in the area for longer periods every year. In 1978, for the first time in the Netherlands in at least 300 years, a single breeding pair was recorded here (Poorter 1980). Up till the late 1990s, the number of breeding pairs did not exceed five pairs in any year (Fig. 2; van der Kooij & Voslamber 1997). Following the creation of freshwater pools and ditches in the formerly dry border zone, the number of breeding birds started to increase from 2000 onwards, until reaching a provisional maxi-

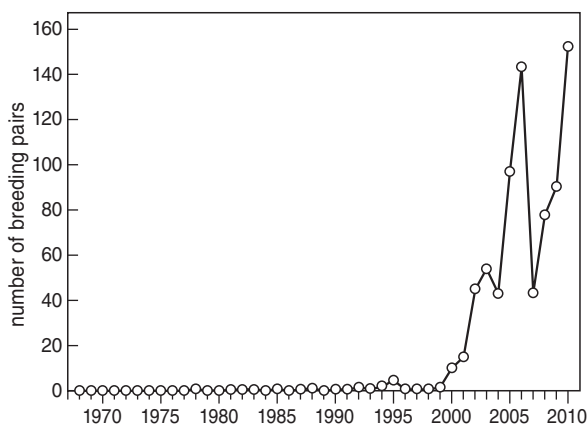


Figure 2. Number of breeding pairs of Great Egrets in Oostvaardersplassen, 1968–2010. Source: RWS Waterdienst (Mennobart van Eerden, Mervyn Roos and others), SOVON, Bijlsma (2008).

mum of 143 pairs in 2006 (Fig. 2). Numbers in the Oostvaardersplassen dropped steeply to 43 pairs in the following year when drought and dike leakage caused widespread desiccation of feeding grounds. The breeding population recovered in subsequent years (Bijlsma 2008, van Dijk *et al.* 2010) to reach a new high at 154 pairs in 2010.

During the early years of settlement (between 1977 and 1996), the birds bred successfully on several occasions (4 young in 1978, 1–2 young in 1981, and in 1985 at least 1 young, in all instances from one nest; van der Kooij & Voslamber 1997). All pairs bred in colonies of Eurasian Spoonbill or Grey Heron in the large reed beds in the marsh. In other years breeding was suspected, but the pairs were probably not successful (Zijlstra 1994, van der Kooij & Voslamber 1997). In 1981 and maybe in 1982, 1983 and 1987, mixed pairs with Grey Herons bred successfully in the marsh, while during the same period occasional pairs started to breed elsewhere in The Netherlands (van der Kooij & Voslamber 1997). In the early 2000s, chick production increased steeply, with an estimated minimum of 20, 25 and 45 juveniles fledging in 2000, 2001 and 2002, respectively (M. Zijlstra, pers. comm.).

Feeding habitat

The main feeding patches were situated inside the nature reserve, both in marshland area and in grassland. The egrets showed a distinct preference for water bodies with clear water. In 1987 to 1990 the most important site was the experimental area ‘Waterlanden’ (Table 1), where from March to July feeding was largely confined to the ditches. In August about half of the feeding time was spent in shallow pools, the other half in dry grassland (Table 2). When in 1991 the water level in the western part of the marsh was raised, a large feeding area became available and the birds switched feeding location accordingly (Table 1).

Since the late 1990s, the newly created pools and inundated areas offered additional feeding opportunities, which were readily taken by the egrets. From less than 1 ha in 1988, this habitat increased in size to 23 ha in 1996 and 297 ha in 2000. Likewise, the surface area of inundated grassland increased from 23 ha in 1988, 67 ha in 1996 to 113 ha in 2000. Due to the simultaneously increasing grazing pressure by large herbivores, the grasslands became more and more open, with fewer and smaller patches of rough herbage in spring (March–May), for instance resulting in a decline in numbers of Common Vole (Bijlsma 2008).

The presence of shallow clear water is of increasing importance to the egrets, especially in the first part of

the breeding period (van Eerden & Zijlstra, unpubl. obs.). The importance of the marsh as a feeding area, although declining in relative terms (Table 1), is still evident throughout the year, but especially during summer and early autumn.

Food choice

In the experimental area ‘Waterlanden’ Great Egrets were mainly foraging along the edges of ditches, where they used the ‘walk slowly’ method (Voisin 1991). Three-spined Stickleback *Gasterosteus aculeatus* and other small fishes of 2–10 cm and tadpoles of 2–9 cm were the main prey (91.4% of all prey items; Table 3). Marsh Frogs *Rana ridibunda* were caught as adults (0.8%) or as tadpoles of up to 9 cm (5.7%). Insects and their larvae were taken throughout the season, but only in low numbers (1.6%).

Within the marshland zone Great Egrets were mainly foraging along the borders of large reed beds. The birds were rarely observed in the centre of the larger shallow water bodies. As in the ‘Waterlanden’ they were

Table 1. The proportion of Great Egrets foraging in different habitats in the Oostvaardersplassen area in 1987–2002, as recorded in the field and during monthly aerial counts. From 1987–90, the western part of the marsh was in the dry phase, but had become wetter in 1991–92.

	Marsh	Water-landen	Border zone	Markermeer	n
1987–1990	30.8	38.8	29.4	0.9	214
1991–1992	55.3	9.4	34.6	0.6	159
1993–1996	77.4	11.3	7.0	4.2	71
1997–2000	63.1	23.5	13.4	0	179
2001–2002	54.7	30.7	14.6	0	492
Total	53.0	26.8	19.6	0.5	1115

Table 2. Seasonal use of feeding habitats (%) by Great Egrets in the experimental area Waterlanden, Oostvaardersplassen, based on 1450 observation hours (1989–90).

	Ditches	Shallow water	Dry grassland
March	100	0	0
April	100	0	0
May	98	2	0
June	95	2	3
July	95	5	0
August	10	40	50

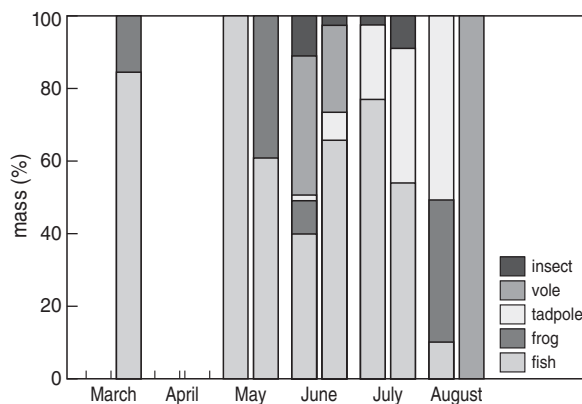


Figure 3. Seasonal shift by two-week periods of prey mass taken by Great Egrets in the Waterlanden, Oostvaardersplassen, 1989 and 1990.

hunting by the ‘walk slowly’ method, almost exclusively focused on sticklebacks (mainly Three-spined) with an occasional insect (less than 1% of all food items). Common Voles were taken in the grassland areas by the ‘stand-and-wait’ method (Voisin 1991), involving small numbers only (0.6% of food items).

From March to May, birds in ‘Waterlanden’ were almost exclusively feeding on fish (Fig. 3). Later on, the proportion of frogs and tadpoles in the diet increased, while in August Common Vole was the most important prey species. Vole feeding occurred less often after 1992.

At least one bird was often seen feeding near fishing boats along the borders of Lake Markermeer. This was mostly observed in July, never during the breeding period and not in 1991. The bird took dead and dying

Table 3. Prey species of Great Egret in Oostvaardersplassen.

Fish	Three-spined Stickleback <i>Gasterosteus aculeatus</i> Ten-spined Stickleback <i>Pungitius pungitius</i> Perch <i>Perca fluviatilis</i> Roach <i>Rutilus rutilus</i> Carp <i>Cyprinus carpio</i>
Amphibians	Common Toad <i>Bufo bufo</i> Common Frog <i>Rana temporaria</i> Marsh Frog <i>Rana ridibunda</i> Edible Frog <i>Rana ‘esculenta’</i>
Water beetles	<i>Hydrous piceus</i> <i>Dytiscus marginalis</i>
Dragonfly larvae	<i>Odonata</i> spp.
Water bugs	Heteroptera spp.
Mammals	Common Vole <i>Microtus arvalis</i>

fishes from the water surface by landing on the surface and prey were swallowed while flying. In this way several fishes were taken in a single flight. Species taken in this way were Perch *Perca fluviatilis* and Roach *Rutilus rutilus* of 10–20 cm length. Following vessels occurred less often after 1992 (Table 1).

Intake rate

Intake rate of the egrets showed considerable variation, depending on the type of prey species (Table 4). The number of prey, as well as the mass caught per minute, was almost similar for stickleback and tadpoles. The intake rate in the experimental area 'Waterlanden' was half of that in water bodies in the marshland (sticklebacks, Table 4). Frogs and voles were caught in smaller numbers per minute, but because of their higher dry mass the intake rate in kJ per minute was much higher than for sticklebacks or tadpoles (Table 4). The bird feeding on fish discards was able to take some relatively large fishes in a very short time, resulting in a high energy intake rate (Table 4). This bird was often seen

Table 4. Intake rates by Great Egrets by prey species and area. WL = experimental area Waterlanden, OVP = marshland zone Oostvaardersplassen.

	Intake rate (n/min)	Caloric value (kJ/g dry mass)	Average dry mass (g)	Intake rate (kJ/min)
Sticklebacks WL	1.1	17.2	0.4	7.6
Sticklebacks OVP	2.1	17.2	0.4	14.5
Frogs WL	0.7	19.6	3.0	41.2
Tadpoles WL	1.2	13.9	0.2	3.5
Voies	0.1	21.4 ^a	9.8 ^a	21.0
Larger fish	0.6	17.6	8.8	92.4

^aAfter Masman *et al.* (1986).

Table 5. Estimated foraging time per day to meet own energy requirements for Great Egrets feeding on different prey species. See text for explanation. WL = experimental area Waterlanden, OVP = marshland zone Oostvaardersplassen.

Prey	Foraging time (min/day)
Stickleback WL	179
Stickleback OVP	94
Frogs WL	33
Tadpoles WL	388
Vole	65
Large fish	15

resting along the dike or in the marsh for quite extensive periods, interspersed with short feeding bouts when small prey items like water bugs *Sigara* sp. with a length of approximately 5 mm were taken.

DISCUSSION

Great Egret numbers in Oostvaardersplassen remained at a low level for 25 years. The 'Great Leap Forward' coincided with the creation of shallow foraging grounds in the border zone of Oostvaardersplassen, within short range of the breeding sites in the marsh. Our study on food and feeding habits of this newly settled population indicates that access to nearby foraging grounds may have been the trigger to the marked increase in breeding pairs since the early 2000s.

Large differences in intake rate, related to prey choice, feeding technique and habitat choice, had a large impact on the daily feeding rhythm of individual birds. The daily needs of an egret were calculated on the basis of its basal metabolic rate (BMR), here expressed as $BMR = 307.6 BW^{0.734}$ (Aschoff & Pohl 1970), an assimilation efficiency of 0.8 for piscivorous birds (Castro *et al.* 1988) and an average body mass of 1250 gram (based on data in Bauer & Glutz von Blotzheim 1966), i.e. at $3 BMR = 1358.8$ kJ. This estimate indicates that, when feeding on stickleback in 'Waterlanden', a Great Egret had to forage for about 3 hours a day to meet its energetic requirements (Table 5). While feeding on the same prey species in the marshland zone of Oostvaardersplassen, after inundation of the marsh, the birds required only about 1.5 hour (Table 5). A bird feeding on larger fish near fishing vessels was able to catch enough food in only 15 minutes time, although this fishing technique probably implies considerably higher energetic costs as flying is a factor 10 more costly than 'standing and waiting' or 'walking slowly' (Voisin 1991). Moreover, competition with the larger Grey Herons made this foraging technique less attractive. It is possible that only specialised individuals were performing this technique, as in recent years it is hardly ever observed.

With progressing season, the birds spent an increasing proportion of their time on resting and preening, presumably coinciding with a shift in prey choice to larger-sized prey items. This increase in intake rate, as expressed in kJ per unit of foraging time, also enabled successful breeding. In 1987–92, successful breeding was only proved for 1991 when the birds visited the western part of the marsh more frequently than in the preceding years. With a water depth of 10–20 cm, this



Figure 4. Part of the breeding colony of Great Egrets in the Oostvaardersplassen, April 2007. Photo by Mervyn Roos.

area turned out to have become a prime feeding area – with high numbers of young sticklebacks – after several years of drought. Together with high transparency of the water this provided optimal feeding conditions for foraging herons and egrets (Voslamber 1992). Intake rates were well beyond those observed in the experimental area ‘Waterlanden’, and feeding bouts were consequently shorter. During 1991 and 1992, although the numbers of egrets were higher than in previous years, egrets rarely visited either ‘Waterlanden’ or the borders of Lake Markermeer, suggesting that feeding conditions in the marsh were better.

Apparently, profitable food resources for Great Egrets during the breeding season had been in such short supply between 1987 and 1992 that raising chicks was near-impossible. Feeding opportunities proved to be best in shallow and clear waters, which were – at the time – scarce in the border zone and only occasionally available in the marshland zone. In the latter part, turbid conditions prevailed in most years due to a continuous suspension of clay particles from the sediment. After the re-inundation of the western part of the marshland zone in 1991, the next two years

of clear water proved beneficial for feeding Great Egrets, allowing successful breeding in 1991. Afterwards, however, water turbidity increased again. In fact, it was not until the restructuring of the border zone, with a considerable increase of the surface area of shallow and clear water in 1997–99, that breeding numbers started to increase. The importance of these feeding grounds was further demonstrated in 2007, when the border zone became desiccated in early spring and breeding numbers dropped from 143 pairs in 2006 to 43 in 2007 (Fig. 2).

Also elsewhere in Europe, the Great Egret has shown a significant increase since the early 1990s, as in Austria (700 pairs in the Neusiedler See, a doubling since the 1970s and 1980s, BirdLife Austria) and Italy (starting in 2000; Fasola *et al.* 2010). The creation of a new marshland area of a sufficiently large scale and inaccessible to humans may have been one of the underlying factors for the return of the species in The Netherlands. Great Egrets are known to depend heavily on undisturbed, extensive marshland areas (Fig. 4), providing roosting, breeding and feeding habitats within daily flying distance of one another (Hagemeyer &

Blair 1997). The possibilities for a thriving new population in The Netherlands (in Oostvaardersplassen as well as elsewhere) are likely to be closely linked to ecological restoration of large-scale marshland areas and/or the upscaling of small patches of marshland. These larger units should ensure a sufficient degree of habitat differentiation to provide safe and undisturbed breeding grounds and productive feeding habitats, including extensive areas of shallow and clear water with emergent vegetation, throughout the season. The occurrence of additional feeding habitats, such as rough meadows where voles can be caught (Gerritsen & van Dijk 2008), as well as large open waters where fish scavenging is possible, may further enhance the prospects for colonisation. In fact, the recent upsurge in non-breeding numbers, the spread of non-breeders across a wide range of habitats throughout The Netherlands, and its winter hardiness indicate that the Great Egret is a more resilient species than hitherto imagined (Klaassen 2009).

ACKNOWLEDGEMENTS

This paper could only be written thanks to different people who assisted during the fieldwork. We would like to mention Anita Dulos and Kees Koffijberg who did a lot of the fish sampling. Wouter Dubbeldam was responsible for quantifying habitat types using GIS. Furthermore, we would like to thank Marjolein Munsterman, Theo Vulink, Menno Zijlstra and Rob Bijlsma for their comments on earlier drafts of this paper.

REFERENCES

- Aschoff J. & Pohl H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 111: 38–47.
- Bauer K.M. & Glutz von Blotzheim U.N. 1966. *Handbuch der Vögel Mitteleuropas*, Band I. Akademische Verlagsgesellschaft, Frankfurt am Main.
- Beemster N. 1997. Dynamisch waterpeil in de Oostvaardersplassen, effecten op broedvogels in relatie tot vegetatieontwikkeling. *Flevobericht* 400. Rijkswaterstaat, Lelystad.
- Bijlsma R.G. 2008. Broedvogels van de buitenkaadse Oostvaardersplassen in 1997, 2002 en 2007. A&W-rapport 1051. Altenburg & Wymenga, Veenwouden.
- Brouwer G.A. 1954. Historische gegevens over onze vroegere ornithologen en over de avifauna van Nederland. *Ardea* 41: 1–225.
- Castro G., Stoyan N. & Myers J.P. 1988. Assimilation efficiency in birds: a function of taxon or food type? *Comp. Biochem. Physiol.* 92A: 86–151.
- Cornelissen P. & Vulink J.T. 1996. Grote herbivoren in wetlands. Evaluatie begrazingsbeheer Oostvaardersplassen. *Flevobericht* 399. Rijkswaterstaat, Lelystad.
- Cramp S. & Simmons K.E.L. 1977. *Handbook of the birds of the Western Palearctic*, Vol. 1. Oxford University Press, Oxford.
- Del Hoyo J., Elliott A. & Sargatal J. (eds) 1992. *Handbook of the birds of the World*. Vol. 1. Lynx Edicions, Barcelona.
- Dick G., Dvorak M., Grill A., Kohler B. & Rauer G. 1994. *Vogelparadies mit Zukunft? Ramsar-Bericht 3 Neusiedler See – Seewinkel*. Umweltbundesamt, Wien, pp. 198–207.
- Dubbeldam W. & Zijlstra M. 1996. Ganzen in Oostelijk- en Zuidelijk Flevoland, 1972/73–1991/92. *Flevobericht* 385. Rijkswaterstaat, Lelystad.
- Fasola M., Rubolini D., Merli E., Boncampagni E. & Bressau U. 2010. Long-term trends of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. *Pop. Ecol.* 52: 59–72.
- Gerritsen G. & van Dijk J. 2008. Grote aantallen veldmuispredatoren in de polder Mastenbroek in het seizoen 2007/2008. *Vogels in Overijssel* 7: 4–18.
- Hagemeyer W.J.M. & Blair M.J. (eds) 1997. *The EBCC atlas of European breeding birds: their distribution and abundance*. Poyser, London.
- Klaassen O. 2009. Slaapplaatstellingen van Grote Zilverreigers. *SOVON-Nieuws* 22(2): 10–11.
- Loonen M.J.J.E., Zijlstra M. & van Eerden M.R. 1991. Timing of wing moult in Greylag Geese *Anser anser* in relation to the availability of their food plants. *Ardea* 79: 253–260.
- Masman D., Gordijn M., Daan S. & Dijkstra C. 1986. Ecological energetics of the Kestrel: Field estimates of energy intake throughout the year. *Ardea* 74: 24–39.
- Poorter E.P.R. 1980. De zilverreigers van de Oostvaardersplassen. *Lepelaar* 66: 23–24.
- van Dijk A.J., Boele A., Hustings F., Koffijberg K. & Plate C.L. 2010. Broedvogels in Nederland in 2008. SOVON-monitoringrapport 2010/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- van Eerden M.R., Lenselink G. & Zijlstra M. 2010. Long-term changes in wetland area and composition in The Netherlands affecting the carrying capacity for wintering waterbirds. *Ardea* 98: 265–282.
- van der Kooij H. & Voslamber B. 1997. Aantalsontwikkeling van de Grote Zilverreiger *Egretta alba* in Nederland sinds 1970 in een Europees perspectief. *Limosa* 70: 119–125.
- van Turnhout C.A.M., Hagemeyer E.J.M. & Foppen R.P.B. 2010. Long-term population developments in typical marshland birds in The Netherlands. *Ardea* 98: 283–299.
- Vera F.W.M. 1988. De Oostvaardersplassen: van spontane natuuruitbarsting tot gerichte natuurontwikkeling. IVN & Grasduinen-Oberon, Amsterdam.
- Voisin C. 1991. *The Herons of Europe*. Poyser, London.
- Voslamber B. 1992. Zilverreigers *Egretta* sp. in de Oostvaardersplassen in 1991. *Limosa* 65: 89–92.
- Voslamber B. 1996. Effecten van waterpeilbeheer en begrazing op het voorkomen van visetende vogels. *Levende Natuur* 97: 4–10.
- Vulink J.T. 2001. Hungry herds. Management of temperate lowland wetlands by grazing. *Van Zee tot Land* 66.
- Wiggins D.A. 1991. Foraging success and aggression in solitary and group-feeding Great Egrets *Casmerodius albus*. *Colonial Waterbirds* 14: 176–179.
- Zijlstra M. 1994. Grote Zilverreigers *Egretta alba* in Nederland en de Oostvaardersplassen. *Vogels in Flevoland* 2: 20–26.

SAMENVATTING

De Grote Zilverreiger *Casmerodius alba* was in de 19de eeuw bijna geheel uit Nederland verdwenen. Sinds de jaren zeventig van de 20ste eeuw neemt de soort hier weer in aantal toe. In de eerste 25 jaar van de hervestiging was er nauwelijks sprake van populatiegroei. Vanaf 2000 echter nam in de Oostvaardersplassen het aantal broedparen plotseling snel toe naar een voorlopig maximum van 154 paren in 2010. Deze ontwikkeling volgde op het beschikbaar komen van een flink areaal nieuw, helder en ondiep moerasgebied in de aanvankelijk droge randzone in 1997. Gedurende de eerste periode van vestiging met stagnerende populatiegroei (1975–99) is in de Oostvaardersplassen de voedsleecologie van de vogels onderzocht om na te gaan welke factoren van belang zijn voor een gezonde populatie. Waarnemingen aan foeragerende vogels werden uitgevoerd in de jaren 1987–92. De Grote Zilverreigers foerageerden vooral in het natuurreservaat. Van mei tot juni zochten ze hun voedsel in sloten, vanaf augustus langs de rietoevers van ondiepe poelen en in het droge grasland. In de sloten vormden Driedoornige

Stekelbaarsjes *Gasterosteus aculeatus*, andere kleine visjes, kikkers en kikkervissen het belangrijkste voedsel (91,4% van alle prooien). In de ondiepe poelen ving de vogels bijna uitsluitend stekelbaarsjes en in het grasland Veldmuizen *Microtus arvalis*. Eén vogel foerageerde achter vissersboten, waar hij 10–20 cm grote Baarzen *Perca fluviatilis* en Blankvoorns *Rutilus rutilus* ving. Een Grote Zilverreiger die stekelbaarsjes vangt, moet 1,5 tot 3 uur foerageren om zijn dagelijkse behoefte gedekt te krijgen. Voor een vogel die de vissen achter vissersboten oppikt, zijn 15 minuten foerageren al voldoende. De vogel die deze tactiek toepaste, verloor echter veel energie met vliegen. Voor het merendeel van de Grote Zilverreigers vormen ondiepe, heldere sloten en poelen met voldoende jonge stekelbaarsjes en dekking door rietoevers en opgaande waterplanten de optimale voedselhabitat. De belangrijkste oorzaak voor de recente explosieve groei van de broedpopulatie is dus waarschijnlijk te vinden in de aanleg van het nieuwe moeras met helder water in de randzone, binnen vliegafstand van de ongestoorde en ontoegankelijke broedplaatsen. Deze bevindingen zijn van belang voor het uitvoeren van ecologisch herstel van wetlandssystemen elders in Nederland.

Appendix 1. Length (L, mm) – mass (M, g) relations for fish and tadpoles in the experimental area Waterlanden, Oostvaardersplassen.

Species	Equation
Three-spined Stickleback	$^{10}\log(M) = -5.307 + 3.175 \times ^{10}\log(L)$
Ten-spined Stickleback	$^{10}\log(M) = -4.673 + 2.745 \times ^{10}\log(L)$
Carp	$^{10}\log(M) = -4.959 + 3.044 \times ^{10}\log(L)$
Roach	$^{10}\log(M) = -5.250 + 3.112 \times ^{10}\log(L)$
Perch	$^{10}\log(M) = -5.430 + 3.250 \times ^{10}\log(L)$
Tadpole	$^{10}\log(M) = -3.636 + 2.264 \times ^{10}\log(L)$



Great Egrets in the nature reserve Oostvaardersplassen, The Netherlands (October 2007). Photo by Mervyn Roos.